Scanning, biases, and inhibition to visual stimuli in healthy and right hemisphere lesioned adults.

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Abstract

This thesis explores right hemisphere involvement in perceptual biases to chimeric faces and posterior right hemisphere involvement in response inhibition through an examination of the role of eye movements.

Studies of patients with focal brain lesions and neuroimaging research indicate that face processing is predominantly based on right hemisphere function. Additionally, experiments using chimeric faces, where the left and the right hand side of the face are different, have shown that observers tend to bias their responses toward the information on the left. A series of experiments were conducted using lifelike gender based chimeric faces (Burt and Perrett, 1997) to explore the relationship between eye movements and perceptual biases.

A left perceptual bias was observed in experiment 1, in that subjects based their gender decision significantly more frequently on the left side of the chimeric faces. Additionally, analysis of the eye movement patterns indicated a strong tendency to first fixate on the left side of the image and subsequently a relationship between perceptual biases and eye movements.

Experiment 2 examined the issue of inversion of such facial stimuli and provided evidence that the right hemisphere may still be more influential in determining gender from inverted chimeric stimuli, as a significant left perceptual bias was demonstrated to these types of stimuli. It is proposed that the chimeric bias effects found in this experiment argue against the idea that inversion destroys the right hemisphere superiority for faces.

Whilst experiments 1 and 2 provided evidence for right hemisphere dominance in the processing of chimeric faces, experiments 3 and 4 investigated the influence of eye movements and exposure duration in

modulating the bias. Experiment 3 and 4 demonstrate that in younger adults but not older adults that a reliable leftward bias can be obtained when stimuli are exposed for brief durations only. However, evidence is provided that indicates that the perceptual bias is enhanced in the presence of eye movements. Additionally, experiment 4 shows that the perceptual bias is demonstrably diminished in older adults, possible mechanisms for this finding are discussed.

Experiment 5 reviews evidence related to dysfunction in visual search in patients with right hemisphere lesions, however what is less well understood is how well such patients are able to inhibit a response in an otherwise simple search task. Experiments 5 and 6 explore oculomotor capture in such patients. Patients were asked to search for a colour target amongst distracters and to signal target location with a saccade. On each trial an additional distracter was presented which could be either similar or dissimilar to the target and appear either with or without a sudden onset. Patients were demonstrated to have higher oculomotor capture rates by the additional distracter, and to be more susceptible to the distracting influence of sudden onsets.

Experiment 7 employed an antisaccade task and a fixation task and demonstrated in the same group of patients further impairments in response inhibition. In both tasks patients were demonstrated to have significant difficulty in inhibiting an eye movement to a peripheral distracter (relative to age matched controls). Results of experiments 5-7 indicate that patients with right hemisphere lesions that spare the frontal lobe have demonstrable impairments in inhibiting responses to suddenly appearing peripheral stimuli, implicating a role for posterior brain structures in this type of inhibition.

Declaration

This thesis has been composed by the undersigned. It has not been submitted or accepted in any previous application for any degree at this or any other university. The thesis has been completed by myself unless otherwise indicated in the text.

Stephen Hugh Butler

For Nina, MLK

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Previous published dissemination

Findings reported in experiment 1 has been previously presented at the European Conference of Visual Perception, Paris, France (2003), and subsequently published:

> Butler S, Gilchrist ID, Burt DM, Perrett DI, Jones E, & Harvey M. (2003) Eye-movement patterns reflect perceptual biases apparent in chimeric face processing. *Perception*, (32), 57.
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> Butler S, Gilchrist ID, Burt DM, Perrett DI, Jones E, & Harvey M. (2005) Are the perceptual biases found in chimeric face processing reflected in eye-movement patterns? *Neuropsychologia*, 43, 52-59.

Findings reported in experiment 2 have been published:

> Butler S. & Harvey M. (2005) Does inversion abolish the left chimeric face processing advantage? *Neuroreport*, 16, 1991-1993.

Findings reported in experiment 3 have been presented at the annual meeting of the Cognitive Neuroscience Society, New York (2005), and subsequently published:

> Butler S, & Harvey M. (2005) Scanning bias enhancement of the perceptual biases found in chimeric face processing. *Journal of Cognitive Neuroscience*, (SS), 44-45.
>
> Butler S, & Harvey M. (2006) Perceptual biases in chimeric face processing : eye-movement patterns cannot explain it all. *Brain Research*, 1124, 96-99.

Findings reported in experiment 4 with regard to older adults have been presented at the annual meeting of the Cognitive Neuroscience Society, New York (2005):

> Butler S, & Harvey M. (2005) Scanning bias enhancement of the perceptual biases found in chimeric face processing. *Journal of Cognitive Neuroscience*, (SS), 44-45.

Findings reported in experiment 5 have been presented at the European Conference of Visual Perception, Budapest, Hungary (2004), and subsequently published:

> Butler S, Ludwig CJH, Gilchrist ID, & Harvey M. (2004) Oculomotor capture in a patient with a unilateral right temporo-parietal lesion. *Perception*, (33), 129.
>
> Butler S, Gilchrist ID, Ludwig CJH, Muir K, & Harvey M. (2006) Oculomotor capture in a patient with a right tempero-parietal lesion. *Cognitive Neuropsychology*, 23, 990-999.

Findings reported in experiment 6 have been presented at the European Conference of Visual Perception, Paris, France (2003):

> Harvey M, Gilchrist ID, Butler SH, Ludwig CJH, & Muir K. (2003) Impairments of goal and stimulus driven control in patients with right fronto-parietal lesions. *Perception*, (32), 37.

Findings reported in experiments 6 and 7 have been collectively presented at the European Conference of Visual Perception, St Petersburg, Russia (2006), and the annual meeting of the European Brain and Behaviour Society, Dublin, Ireland (2006).

> Butler SH, Ludwig CJH, Gilchrist ID, Muir K, Bone I, Reeves I, Duncan G, Harvey M. (2006) Evidence from converging paradigms for posterior cortical involvement in response inhibition. *Perception*, (35).
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> Butler S, Ludwig CJH, Gilchrist ID, & Harvey M. (2005) Parietal lobe involvement in response inhibition. *Acta Neurobiologiae Experimentalis*, (65), 30.
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> Harvey M, & Butler S. (2005) Parietal lobe contributions to stimulus and goal driven search, evidence from brain-lesioned populations. *Acta Neurobiologiae Experimentalis*, (65), 21.

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Chapter 1

Introduction

A right hemisphere bias for face processing has been consistently reported in the literature both within cognitive psychology (Dutta & Mandal, 2002; Hugdahl, Iversen & Johnsen, 1993; Rhodes, 1993) and neuroimaging (Horwitz, Grady, Haxby, Schapiro and Rapoport (1992), Kanwisher, McDermott & Chunn, 1997, Ishai, Schmidt, & Boesiger, 2005) research. Split visual field studies have, for example, consistently reported that facial stimuli presented to the right hemisphere (left visual field) are both processed faster (e.g. Dutta & Mandal, 2002), and more accurately (e.g. Hugdahl, Iversen & Johnsen, 1993), than facial stimuli presented to the left hemisphere (right visual field).

From the patient literature, although bilateral lesions were originally implicated (Meadows, 1974; Damasio, Damasio, & van Hoesen, 1982) in the development of prosopagnosia, a dysfunction in the recognition of familiar faces (see e.g. Farah, Wilson, Drain & Tanaka, 1995), more recent work has indicated that right hemisphere lesions alone are sufficient to cause the condition (De Renzi, 1986, Landis, Cummings, Christen, Bogen, & Imhof, 1986, De Renzi, Perani, Carlesimo, Silveri, & Fazio, 1994, Uttner, Bliem & Danek, 2002).

Since Wolff first wrote on the more 'acceptable' nature of the right side of the human face in 1933, considerable research has been conducted investigating apparent hemispheric asymmetries in face processing, commonly by employing a chimeric face paradigm. Wolff's initial findings were later more fully replicated by McCurdy (1949) and Lindzey, Prince & Wright (1952). The 'Wolff split face technique' employs composite facial stimuli comprising a pair

of mirror image left and right halves of the face presented alongside the original whole face. Participants indicate which of the chimerics is more like the original whole face. Both McCurdy (1949) and Lindzey et al (1952) reported a bias to choose the image composed of the left side of the face as perceived from the viewpoint of the participant.

Somewhat more recently Gilbert & Bakan (1973) proposed that the phenomenon was a product of the perceiver rather than a characteristic of the face itself, as originally concluded (e.g. Lindzey et al, 1952). Gilbert & Bakan returned to the Wolff split face technique, but in addition participants were invited to compare the two composite left-mirror left and right-mirror right images to the *mirror image* of the whole face. The perseverance of the left bias in participants selections led them to conclude that the bias was a wholly endogenous phenomenon. This study has since been successfully replicated (e.g. Rhodes, 1985).

Following the finding of Wolff (1933) that the right side of the human face shows more correspondence to "the impression caused" by the full face, and the findings reported above, the finding of a robust left perceptual bias for chimeric images has been reported with chimeric stimuli employing emotion (David, 1993), gender (Luh, Rueckert & Levy, 1991), age and attractiveness (Burt & Perrett, 1997). When the left and the right hand side of a face are different (chimeric), observers tend to bias their responses toward the information contained in the left side of the face. Recently, Failla, Sheppard & Bradshaw (2003) presented evidence that the perceiver bias induced by chimeric faces is detectable from 5 years of age but weakened in subjects over 60. Interestingly, the left bias for the processing of facial stimuli has been demonstrated to be so robust that it can be generated when the facial stimulus is passed behind a narrow vertical slit, allowing only a fraction of the

image to be seen at any one time, thus requiring the perceiver to recreate the whole image internally (Grega, Sackeim, Sanchez, Cohen & Hough, 1988). Indeed the effect can even be demonstrated via the internet (Rueckert, 2005). Brady, Campbell & Flaherty (2005) have recently provided evidence that such perceptual asymmetries are held in long term memory for the identification of very familiar faces, when chimeric images are employed.

The bias can also be demonstrated when subjects are required to match faces to names. Yamamoto, Kowatari, Ueno, Yamane & Kitazawa (2005) exposed subjects to photographs of famous people in either three quarter left or right views (from the face owners perspective), constructed so that the relevant eye was in the centre of the picture. Subjects had to decide whether the face matched a presented name. Stimuli were presented at sub saccadic thresholds. Reaction time analysis indicated that people were quicker to identify faces as matching names with faces presented in left three quarter view compared to right three quarter view. The authors point out that the important facial features such as nose and mouth in the left three quarter view were located in the left visual hemifield whilst the same features in the right three quarter view were in the right hemifield.

The findings above were also complimented by an imaging study. Kowatari et al (2004) conducted a study employing fMRI, where they exposed subjects to photographs of famous people again in three quarter view. In this study subjects were simply required to think about whether or not they recognised the person. Comparison of BOLD signals from both types of view indicated that left view images minus rightward view images induced significant activation in right prefrontal cortex and right inferior parietal cortex, whilst no activation was revealed by the opposite contrast. They point out that the prefrontal cortex in this context enhances the efficiency of the

temporal lobe face memory system. Kowatari et al suggest that the left three quarter view activates the memory retrieval system more strongly, which they believe explains the results of Yamamoto et al (2005).

A bias just for faces?

However, it is possible that this right hemisphere bias may not reflect a 'pure' facial processing advantage but rather a general right hemisphere advantage for the processing of any given intricate visual stimulus. Nicholls & Roberts (2002) reported significant left perceptual biases in their 'Greyscales' luminance decision task, which required subjects to decide which of two identical, but mirror opposite bars was the darker. Similar results were reported in normal children but not children diagnosed as displaying attention deficit hyperactivity disorder (Klimkeit, Mattingley, Sheppard, Lee & Bradshaw, 2003). Luh, Reuckert & Levy (1991) examined non-facial chimeric stimuli that required subjects to estimate which of two paired identical (but rotated) shapes was the most rounded in one condition or contained the most dots in a second condition. A significant left field bias was found for the dots decision but not for the roundness decision. Gooding and Tallent (2002) also obtained significant leftward perceptual biases for quantity decisions to rectangles filled with dots and also for greyscale filled rectangles.

Therefore it would appear that some, but clearly not all, other forms of visual stimuli enjoy a left field/ right hemisphere advantage. However, some ambiguity is added to the issue with the reported finding of a left field bias for human chimeric faces but not for chimeric faces composed of monkeys (Overman & Doty, 1982).

Difficulty of discrimination

Carbary, Almerigi & Harris (1999, 2001, & 2002) originally hypothesised that perceptual biases to composite and chimeric faces may be related to the difficulty inherent in the task, suggesting that as difficulty of discrimination increases so does the reliance on *right hemisphere* mechanisms to do the task. Carbary, Almerigi & Harris (1999) originally however reported findings that did not support their theory of a relationship between difficulty of discrimination and biases.

In a second study (Carbary, Almerigi & Harris, 2001) they employed paired happy-neutral faces in free view and required subjects to make decisions as to which face was happier and then rate the difficulty of the judgement. They obtained a significant left bias in the task for right handed subjects and reported a small but significant correlation indicating for the majority of stimuli that the easier the judgment the *stronger the left visual field bias*, thus their findings appeared to indicate that as the task became harder *the greater the shift to a right visual hemifield bias.* This effect was far stronger in female subjects. They interpreted from their results that the difficulty of a task is one variable associated with changes from one style of face processing to another, and may reflect a shift from a global holistic right hemisphere process to a more feature based process involving a more local analysis of features. Thus they suggest it is possible that manipulations including inverted face stimuli cause a change from the normal left visual hemifield bias due to their inherent increase in task difficulty. Although other factors such as gender and handedness contribute to changes in lateral biases.

This conclusion was further elucidated in a third study (Carbary, Almerigi & Harris, 2002), which utilised both photographic and cartoon emotion based chimeric stimuli, further subdivided into levels of difficulty of

discrimination. Subjects had to decide which face was happier and afterwards were asked to categorise their decision-making processes. In one of the two experiments conducted the degree of bias was significantly different for the two levels of difficulty in the photographic condition (and in the same direction in the other). Similarly for the cartoon chimerics significant differences in bias were found between levels of task difficulty, with bias reducing with increases in task difficulty.

However, it is of interest to note that Rodway, Wright and Hardie (2003) have recently reported findings which suggest that the strength of perceptual bias in their task, involving discrimination of mild emotional content from purely neutral distractors is *stronger* when the discrimination is more difficult.

Scanning Direction

Despite these strong effects, it has been argued that the left perceptual bias may not purely reflect a right hemisphere processing advantage but rather an interaction between a long practised directional scanning bias of the participants and cerebral lateralisation (Vaid & Singh, 1989). Although Gilbert & Bakan (1973) reported a left perceptual bias in the processing of their chimeric stimuli amongst native Hebrew readers (a language that is scanned from right to left), the magnitude of the effect was reduced in this population. However most of the subjects in this research had begun to be exposed to English by the age of 13. Clearly this is problematic as the degree of exposure to western left to right reading could have an impact on the effect. Vaid & Singh (1989) further suggest that similarities between English and Hebrew such as similar direction in arithmetical and musical notation may make Hebrew unsuitable for studying cerebral lateralisation. Using smiling-neutral chimeric faces, they examined perceptual biases in readers of Hindi

(scanned from left to right), Urdu (scanned from right to left, but considered as bi-directional readers due to exposure to Hindi) and Arabic (scanned from right to left) and reported a significantly greater leftward bias in left to right Hindi readers compared to the other two groups.

However, more problematical for a reading direction induced account of left visual field biases, was the finding that the Arabic readers *did not show a significant bias in the opposite direction.* Their right bias was in fact not significantly different from the bi-directional readers. A pure reading account of the left visual bias effect would demand that the right to left readers show a mirror image of the performance of the left to right readers. Therefore, although an account based purely on a bias that is driven by reading direction is curtailed by this finding, it remains a perfectly reasonable possibility, as suggested by Vaid & Singh, that reading habit interacts in some way with cerebral lateralisation.

Following from this, Sakhuja, Gupta, Singh & Vaid (1996) examined performance of left and right handed readers of Hindi (read from left to right), Urdu (read from right to left) and bi-literates. The task was a which-is-happier decision to emotional chimeric faces in free view. They found that Hindi readers showed a significant left bias, Urdu readers showed a right and billiterates no bias. However, an interaction with handedness indicated a left preference for right handed readers of both Hindi and Urdu, although Hindi readers were significantly more left biased than Urdu right handers.

More recently, further evidence for the involvement of scanning direction in perceptual biases is provided by Heath, Rouhana and Ghanem (2005), who reported increased leftward biases in the perception of facial affect amongst readers of left to right scripts compared to readers of right to left scripts or bi-directional readers. Heath, Mahmasanni, Rouhana & Nassif

(2005) have also reported some evidence of the involvement of scanning direction in aesthetic preferences.

Eviatar (1997) examined the impact of bilingualism and asked subjects to make numeric decisions to bar graph stimuli presented briefly to both fields, a task that Boles (1986) had argued evoked right hemisphere dominance. Subjects were either monolingual Hebrew readers or bilingual Hebrew/Arabic readers. The point of the study was to examine the effect of scanning habit *and* bilingualism. Comparing her findings to those of Boles (who used monolingual English speakers) she reported that responses were faster in the left visual field. She could find no evidence that scanning habits of the subjects had any effect on visual field advantages in the task, and found no effect of bilingualism. She thus concluded that there was no evidence that scanning habits had any effect on the task.

Eviatar (1997) further conducted a chimeric faces test with her subjects as well as a chair identification task, where chairs were briefly flashed to both hemifields and subjects had to pick them out from a subsequent array. Presentation times were titrated in order that only one chair would be accurately identified. Eviatar was interested in whether bilingualism or right to left scanning habits would have an impact on performance. No bias was found in either group in the chimeric faces task and no evidence of scanning habits having an impact on the chair task.

Eviatar points out that Vaid & Singh (1989) suggested that the effect of reading direction could influence perceptual biases due to differences in the allocation of spatial attention between readers of different languages *or* differences in their mental scanning. Results from the chair task show that subjects did not differ from left to right readers in this measure of the allocation of spatial attention. She suggests that scanning habits can be

considered to be constructed of two components, a bias to scan to the first element of the text, and a bias to scan in the direction of the text. Therefore, the first bias is what causes left to right readers to demonstrate biases in the chimeric faces task whereas right to left readers do not, as they are initially biased to the left side of the page.

Eye movements and chimeric faces

Clearly further research into how scanning influences the left perceptual face bias is warranted and one obvious approach is the on-line study of eye movements during chimeric face processing. Surprisingly though, to date little research has been undertaken to examine the relationship between perceptual biases apparent in chimeric face processing and accompanying eye movements. The limited research there is has so far yielded equivocal results.

Gallois et al (1989) exposed participants to facial images composed of one side of the face and its mirror image and requested subjects in one condition to simply gaze at the images for seven seconds and in a second condition to gaze for seven seconds and report the emotional state of the face. In both conditions more first fixations were made to the left and significantly more time was spent fixating on the left.

Mertens, Siegmund & Grüsser (1993) reported that analysis of eye movement behaviour in participants exposed to facial stimuli reveals that the eyes, nose and mouth of stimuli were the preferred inspection targets and reported that subjects spent more time fixating on the left hand side of face stimuli regardless of whether the faces were presented normally or left/right inverted. However, other results do not complement such findings. Grega et al. (1988) obtained a significant left perceptual bias in a task involving

similarity judgements between whole faces and left-mirror left and right-mirror right composite chimeric stimuli. However, when examining eye movements to the whole faces, no consistent directional bias to the first eye movement, no relationship to subsequent perceiver bias, and no asymmetry in gaze duration was found. Using simple, monochrome and emotionally neutral, facial stimuli Phillips & David (1997) reported that their healthy subjects examined the left half of the face first more often when analysed across stimuli. Alternative analysis revealed that this trend remained but was non-significant across subjects. Unfortunately, when exposing participants to chimeric (happy/ sad) line drawings of faces they failed to find a leftward perceptual bias, although eye movement analyses again revealed a significant bias to view the left side of the face first more often across stimuli.

Thus with regard to eye movements there is some evidence that the left side of chimeric faces is inspected first and/or for longer, although in one of those studies non-chimeric faces were used (Mertens et al., 1993) and in another no consistent leftward perceptual face bias was reported (Phillips & David, 1997). The study that found a strong left perceptual bias in chimeric face choice failed to find systematic scanning effects to whole faces (Grega et al, 1988).

The effect of stimuli

One of the reasons for this lack of consistency may be that the studies described employed either simple line drawings or spliced photographs as chimeric faces, thus creating some uncertainty over whether these distorted stimuli are processed in a normal manner. Recent innovations with computer graphics software allows for realistic manipulations of images (Benson & Perrett, 1991, 1993; Brown & Perrett, 1993; Perrett, May & Yoshikawa, 1994;

Rowland & Perrett, 1995; Burt & Perrett, 1995; Frigerio, Burt, Montagne, Murray & Perrett, 2002), ensuring that chimeric face stimuli retain as many characteristics of normal faces as possible, in order to maximise the likelihood that subjects engage in normal face processing when exposed to such stimuli. In this thesis, such subtly blended chimeric images were employed, and in experiment 1 saccadic eye movements made during gender based chimeric stimulus presentation were examined. It is intended to replicate the left perceptual face bias previously reported (David, 1993; Luh, Rueckert & Levy, 1991; Burt & Perrett, 1997). More importantly though, to establish if there is indeed an overall leftward scanning bias for chimeric faces and if there is a relationship between perceptual bias and eye-movement bias. This was assessed by measuring the direction of the first saccade and the number and duration of left and right fixations overall and in relation to the perceptual response made (i.e. whether subjects based their decisions on the right or left half of the chimeric face).

Handedness

All studies will be conducted with right-handed subjects, as the literature strongly suggests that the left visual field bias effect is more robust in this group. Left handed individuals show more variation in terms of cerebral lateralisation (Carbary, Almerigi & Harris, 2001), with variation ranging from large perceptual asymmetries to no evident asymmetry (Luh, Redl & Levy, 1994). Luh et al reported that they did obtain a left perceptual bias in a large sample of left-handers with chimeric facial stimuli, although the effect was somewhat diluted from that obtained in a right-handed sample studied previously (Luh, Rueckert, and Levy, 1991). In a smaller sample

Gilbert & Bakan (1973) reported that their left field bias was only found for right-handed subjects.

Experiment 1: Are the perceptual biases found in chimeric face processing reflected in eye movement patterns?

Method

Participants

Twenty participants (16 female and 4 male, mean age 22.5, S.D.=3.4) took part in the study on a voluntary basis. They were all right handed as assessed by the Annett Handedness Inventory (Annett, 1970) and had normal or corrected to normal vision.

Materials and stimuli

a) Manufacture of stimuli

Forty faces were created for use in the study: 10 pairs of male and female blended stimuli and 10 pairs of chimeric male/female and female/male stimuli. Each gender blend was composed of photographs of a number of different individuals, with both the photographic conditions and the age of people photographed in each pair of blends approximately matched. Each blend image was rotated and scaled to match eye position across the pair, stretched vertically to match the middle of the mouth and made symmetrical across the blend's midline.

A pair comprising of one male blend and one female blend image was used to manufacture a pair of chimeric stimuli. The first of the pair was created by a merging of the female face blend on the left and the male face blend on the right. The merging process involved a gradual change in shape and colour from one image to the other across the vertical midline, producing

a seamless merger. The second chimeric stimulus of the pair was a mirror image of the first (Benson & Perrett, 1991; Burt & Perrett, 1997).

b) Manufacture of single gender blended stimuli:

Twenty different gender blended stimuli (10 male, 10 female) were created (see Table 1.1).

Table 1.1: Description of single gender blended stimuli.

Image	Description
Image 1	Derived from two male face blends; a blend composed of the 15 faces rated[1] as most attractive from a population of 59 males aged 20-30, and a blend from the 15 faces rated least attractive[3].
Image 2	Derived from two female face blends; a blend composed of the 15 faces rated[1] as most attractive from a population of 60 females aged 20-30, and a blend from the 15 rated least attractive from the same population, matched in height to the most attractive blend.
Image 3	The high attractiveness rating[1] male face blend used to make Image1.
Image 4	The high attractiveness rating[1] female face blend used to make Image 2[4].
Image 5	Derived from 13 white Caucasian males with an average age of 68.
Image 6	Derived from 30 white Caucasian females with an average age of 68.
Image 7	Derived from 9 Jamaican boys, all aged 10 years.
Image 8	Derived from 10 Jamaican girls, all aged 10 years.
Image 9	Derived from 10 Caucasian boys, all aged 10 years.
Image 10	Derived from 10 Caucasian girls, all aged 10 years.
Image 11	Derived from 20 white Caucasian boys, all aged 8 years.
Image 12	Derived from 20 white Caucasian girls, all aged 8 years.
Images 13-20	Composed of four groups of male and female students each aged between 20-24 years. Each composite group contained at least 15 individual students[2].

[1]See Burt and Perrett (1997) for the rating procedure used for these stimuli.
[2]See Frigerio et al (2002).
[3]To ensure that the features of the two blends coincided across the midline, the low attractiveness blend was stretched in height to ensure that the distance from the mouth to the midpoint between the eyes matched those of the high attractiveness blend.
[4]The female face blend was stretched in height to ensure that the distance from the centre of the mouth to the midpoint between the eyes matched those of image 3.

Following blending, each face was made symmetrical using the 'Feature Point' system described by Burt & Perrett (1997). This approach ensures that the eyes of the image are placed in standard positions and that the shape of the face is symmetrical.

c) Manufacture of chimeric face stimuli

Two gender blend images (one male and one female) were combined into a chimeric stimulus using the 'Mask Technique' described by Burt & Perrett (1997). This method adopts an approach in which shape and image colouration are gradually faded across the midline of the image, so that a seam cannot be discerned. The resulting stimuli were pairs of chimeric faces with the left and right halves differing in relation to gender. Example stimuli can be seen in Figure 1.1.

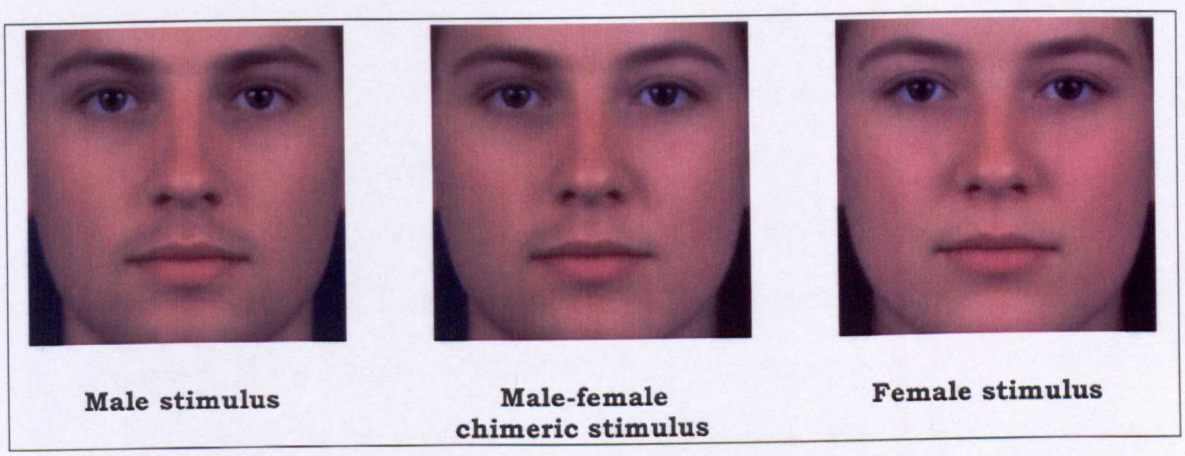


Figure 1.1: Example of a stimulus configuration

d) Eye movement and response data acquisition

Chimeric and whole faces were presented on an IBM compatible personal computer (133MHz Desktop Pro) attached to a 17-inch SVGA monitor. The programs controlling the displays were written in-house.

Participants were instructed and shown the response pad, which consisted of a green button (marked male) denoting a male judgement and a red button (marked female) denoting a female face judgement. Subjects sat with both hands positioned ready to press the keys. The distance between the computer screen and the eyes was 57cm. Subjects sat with their chin on a chin rest and the stimulus was viewed with both eyes. However, only the eye with the best spatial accuracy (as determined following the validation procedure, described below) was analysed.

Face stimuli comprised 10 whole female faces, 10 whole male faces and a further 10 female-male and 10 male-female chimeric faces forming 40 trials per block in which the faces were presented randomly. Each face was preceded by a fixation point, which consisted of a black circle on a grey background with a diameter of 0.3 degrees, presented until fixation was stable. Stable fixation was assessed manually by a real time display of eye position superimposed on the fixation location on another computer that was linked to the eye tracker. Each facial stimulus was presented for two seconds and, following presentation, subjects were asked to indicate the gender by pressing one of the two keys described above. Each participant completed 5 blocks of 40 trials. The purpose of the experiment was not disclosed to participants until the end of the experiment.

Eye movements were recorded with the SMI EyeLink System (SensoMotoric Instruments GmbH, Teltow, Germany) using the centre of the pupil as well as the corneal reflection technique to define pupil position. Each block of trials was preceded by a 9-point grid calibration and validation for which participants were instructed to saccade to a black circle (0.3 deg) on a grey background, which appeared sequentially at nine points in a square array. Between trials, the fixation circle reappeared to correct for drift due to

head movements. Eye movements were recorded at 250 Hz sample rate at a spatial resolution, typically, of 0.3 degrees. Saccade onset was defined as a change in eye position with a minimum velocity of 30 deg per second or a minimum acceleration of 8000deg per sec^2.

Subjects were asked not to make their gender judgement until the face had disappeared in order to allow enough time to meaningfully track the face.

Results

Recording and Response Errors

Due to a recording error in the first block, one of the 21 participants undertook 6 rather than 5 blocks of trials. One participant was omitted due to the participant's consistent failure to follow task instructions. Of the 4000 remaining trials involving whole and chimeric faces 0.8% were omitted due to recording errors.

Out of the 2000 trails in which whole male or female faces were presented, 12% of male and 16% of female faces were incorrectly identified. I did not expect perfect performance on these whole faces as androgynous looking faces were chosen deliberately in order to encourage ocular scanning.

Fixations for whole and chimeric faces

For whole faces 13689 fixations were recorded, 54% to the left and 46% to the right of the screen. Similarly for the chimeric faces, 14452 fixations were recorded, of these 55% were to the left and 45% to the right of the screen. Fixation distributions for whole and chimeric faces can be seen in Figure 1.2.

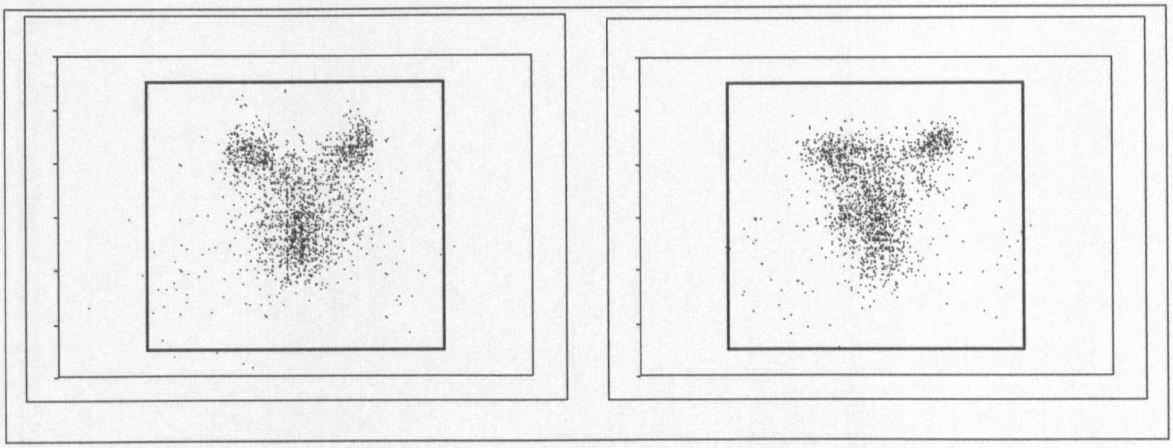


Figure 1.2: Overall fixation distribution for chimeric (left) and whole faces (right).

From this data, there seems to be little indication that chimeric faces were fixated differently from whole faces. Also, although some subjects reported at the end of the experiment that some faces seemed morphed, the majority did not notice. Moreover, as the principle interest of the study was to examine eye-movement patterns to chimeric stimuli no further data regarding the whole face stimuli will be reported.

Analyses of chimeric faces

The following parameters were analysed:

- *Perceptual bias* was assessed by calculating the numbers of times the subjects based their decision on the left part or the right part of the chimeric face.
- *First saccades* were coded in terms of their numbers to the left and right per subject.
- *The total number of fixations* were defined as the left/right fixation proportions per trial averaged for each subject. This procedure avoided the data distortion that would have occurred had I simply calculated the overall number of left/right fixations: this would not take into

consideration that different numbers of saccades were generated in different trials.

- *Fixation duration* was also analysed per trial per subject. I obtained a running total of fixation time by signing leftward fixations as negative and rightward fixations as positive for each sequential saccade in a given trial. This gave a measure of how much more time a subject spent fixating on the left or right side of the screen per trial and again these values were averaged per subject. More time spent on the left was reflected in negative and more time spent on the right in positive values.

Perceptual bias

As expected, information on the left hand side of the face dominated the gender decisions, 62.8% of responses were based on the left side of the chimeric face (binomial test, $p<0.001$).

First saccades

In line with the perceptual bias, analysis of the first saccades again indicated a strong tendency to first inspect the left side of the face. Of 1987 first fixations the majority (75%) were to the left of the screen. A one-sample t-test of the difference between numbers of leftward and rightward first fixations per subject was carried out testing for a difference from zero. This was significant across subjects ($t(19) = 5.22$, $p<0.001$). Furthermore, it was observed that when subjects showed a left behavioural bias (i.e. the left side of the face influenced the gender decision), 77.1% of the first saccades were to the left but with a right behavioural bias 71% of the first saccades were still to the left.

Average proportions of total fixations

For the 20 participants the grand proportion of leftward fixations was 0.55. A one-sample t-test (testing against 0.5) marginally failed to reach significance ($t(19) = 1.99$, $p=0.06$), indicating no reliable difference in the proportions of left and right fixations to the chimeric faces (see figure 1.3).

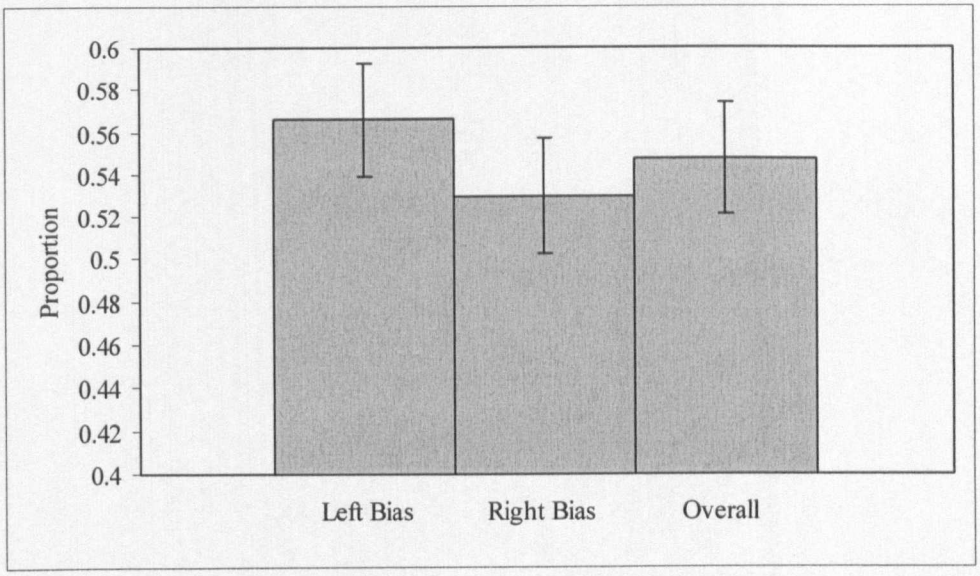


Figure 1.3: Average proportions of leftward fixations per trial per subject, with SE error bars, for left and right perceptual biases, and overall.

However, a somewhat different picture emerged when the proportions of fixations made to the left or right of the screen were examined separately for left and right perceptual biases: a paired samples t-test ($t(19) = 3.47$, $p<0.01$) indicated a significantly greater proportion of leftward saccades with a left perceptual compared to a right perceptual bias. Moreover, the proportion for left fixations with a left perceptual bias proved significantly different from an even 50/50 distribution ($t(19) = 2.47$, $p=0.02$) whereas there was no reliable difference for the right perceptual responses ($t(19) = 1.08$, $p=0.29$). See Figure 1.3 for these differential effects.

Fixation duration

Results of the fixation duration analyses mirrored the total fixation data: overall subjects gave no indication of spending more time on either the right or left side of the chimeric face (see figure 1.4, one-sample t-test: $\underline{t}(19)= 1.50$, $p = 0.15$). But again for left versus right perceptual biases significant differences became apparent (see figure 1.4: paired samples t-test: $\underline{t}(19) = 2.60$, $p=0.02$) with subjects spending significantly more time fixating the left half of the screen when a left perceptual bias was also present.

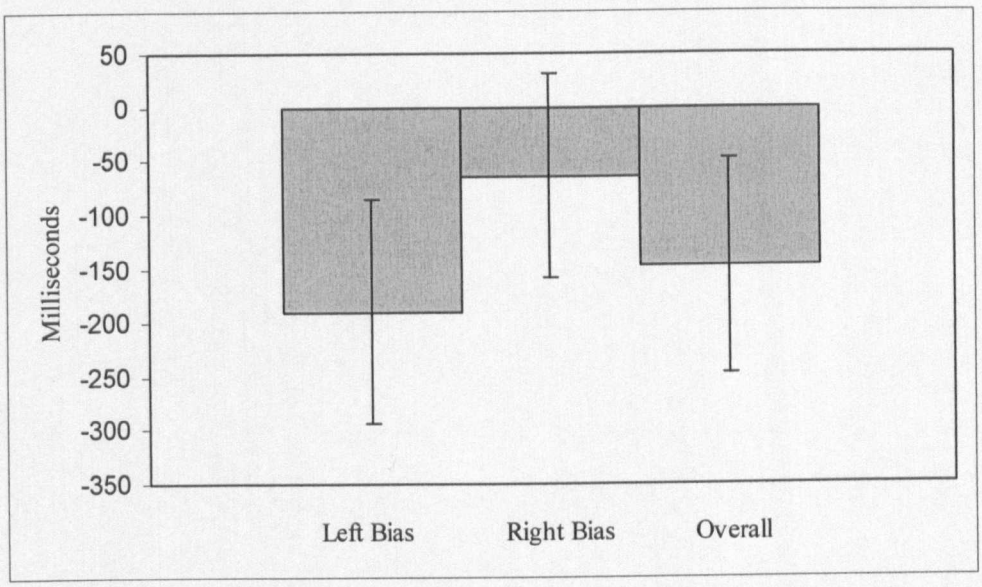


Figure 1.4: Directionally signed (- = left) saccadic gaze duration, with SE mean bars, for left biased chimeric stimuli and right biased chimeric stimuli, and overall.

Discussion

The subjects were given no suggestions as to how to undertake the task but as a group clearly showed a preference to base their decision on the information available in the left visual field. Using subtly blended chimeric images I found clear evidence that subjects used the information from the left

side of the face to inform their gender decisions. This result is clearly in keeping with a long line of research employing chimeric stimuli and indicates that the stimuli behaved as I had expected. This result is particularly satisfying as it is broadly in line with the result for gender decisions obtained by Burt & Perrett (1997) with similar stimuli, and is also in line with other findings of a left perceptual bias for age, attractiveness and emotion (Luh, Rueckert & Levy, 1991; David, 1993; Burt & Perrett, 1997). It further supports a recent complementary finding of left lateralisation for face processing in gender identification tasks employing a new, so called 'Bubbles Technique' (Schyns, Bonnar & Gosselin, 2002).

On-line monitoring of the eye movements during the task allowed further illumination of the processes at work. The strongest finding related to the initial saccade: in line with the data reported by Phillips & David (1997) and Gallois et al. (1989) I found that the first fixation was made to the left hemiface in the vast majority of trials. Indeed overall, three quarters of first fixations were to the left and even when subjects subsequently based their gender decision on the right hand side of the image they still looked to the left initially in 71% of trials.

A first assumption might be that the strong tendency to generate an initial leftward saccade reflects the right hemisphere bias for face processing. However, a leftward saccade results in the majority of the face being in the right visual field and so being projected to the left hemisphere. Indeed one might have expected the opposite effect: the generation of a rightward first fixation so that the majority of the face was in the left visual field. What then underlies this strong counterintuitive first fixation bias? One explanation is as follows. When the face is initially presented, fixation is in the centre of the face. The left hand side of the face projects to the right hemisphere and

activates neural structures that preferentially respond to face stimuli. The same does not occur for the right hand side of the face and so the left hand side of the face is initially more salient, this increased salience results in the bias for a first saccade into that visual field.

Interestingly though, an overall leftward eye movement bias was not found when analysing fixation duration and the number of left and right fixations. This lack of any significant left overall fixation duration bias is in keeping with the results of Grega et al (1988), although they exposed their subjects to their stimuli for a full 6 seconds. However, in contrast to their results I did find a relationship emerging between left perceptual bias and the number and duration of left fixations: a significantly greater proportion of leftward saccades were made when a left perceptual bias was present, whereas no relationship emerged with regard to fixation distributions for right perceptual bias trials. Similarly with regard to fixation duration, again, it was revealed that subjects spent more time fixating on the left side of the screen in trials where they subsequently based their gender decision on the left side of the face. This is somewhat in contrast to the findings of Phillips & David (1997) who reported a non-significant trend for an increase in the fixation duration for stimuli that solicited a right perceptual bias. However, as Phillips & David did not obtain a significant perceptual bias overall with their stimuli such comparisons should perhaps be treated cautiously.

These results therefore argue against the explanation of the left chimeric face bias as an artefact of the long practiced left to right scanning bias of participants in the geographical location in which any of the given research is conducted. If this were the case, I should have found overall leftward eye-movement biases. Instead what I report, are subtle differences in the extent of left or right side scanning that relate to the perceptual response

of the participant. However, one might want to argue that the overwhelming leftward bias in the first fixation is indeed a sign that the left perceptual bias is purely a reflection of the way the majority of people in the western world read. As explained above I would argue instead that the initial fixation reflects the tendency to inspect the side of face better suited to face processing but to solve this issue, eye-tracking studies would have to be run on exclusively right to left reading populations. My interpretation would predict the same leftward bias of first fixations for such populations as for the one in this study, whereas the reading interpretation would predict right initial saccades.

A more comprehensive account of the processes driving the left perceptual and related scanning biases still remains somewhat elusive. As suggested by Burt & Perrett (1997), the findings could reflect a pure right hemisphere specialisation for face processing (but note exception for lip reading). However, the reported findings of, amongst others Luh, Rueckert & Levy (1991) and Nicholls & Roberts (2002) of left perceptual biases for some types of non-facial stimuli undermine this conclusion. It seems plausible that all visual stimuli requiring configurational judgments, once they cross some threshold of complexity, become candidates to generate a lateralised right hemisphere bias (Rhodes, 1993; Burt & Perrett, 1997). Adding further speculation, Burt & Perrett (1997) suggest that processes related to the control of spatial attention hosted within the right parietal lobe may be engaged during visual processing, resulting in a bias to scan the left side of all visual stimuli. It could further be proposed that an interaction of such mechanisms with reading habit is the mechanism explaining the absence of a 'mirror image' result in the perceptual biases demonstrated in readers of right to left scanned languages as reported by both Vaid & Singh (1989) and Gilbert & Bakan (1973) when exposed to chimeric faces. This would also be in keeping with the

results reported by Nicholls & Roberts (2002), who reported significant left perceptual biases in their 'Greyscales' luminance decision task with both English and Hebrew readers. The involvement of an attentional bias in the cognitive processes behind these results was supported by the reported finding that cueing to the right in their Greyscales task reduced the left bias significantly.

Indeed it is already known that patients with hemispatial neglect (whose damage usually includes the right parietal lobe), unlike healthy subjects, base their decisions on the right half of chimeric faces (Mattingley, Bradshaw, Phillips & Bradshaw, 1993). What is less clear is the relationship between this effect and scanning biases and so far only single case studies have been conducted (Walker, Findlay, Young & Lincoln, 1996; Ferber, Danckert, Joanisse, Goltz & Goodale, 2003). Both studies found a rightward bias in fixations for the chimeric stimuli but Ferber et al. (2003) also reported that an alteration of the eye movement pattern with prism adaptation did not change the right perceptual bias.

An interesting question is whether there is a possible temporal component to both the perceptual and eye-movement biases. Phillips & David (1997) suggest that their failure to obtain a clear left perceptual bias with their stimuli might have been due to overexposure to the stimuli at 5 seconds duration. They argue that this may have diluted any initial right hemisphere dominance. Here I reported a clear bias at 2 seconds presentation. However, other evidence suggests that the perceptual bias is fairly resistant to stimulus duration. Burt & Perrett (1997) showed significant biases even when participants had as much time as they wanted to inspect the chimerics. The bias was also present in the earlier literature as an effect of encoding for identity in laboratory conditions (Gilbert & Balkan, 1973). Regarding the eye-

movement effects, Mertens et al (1993) showed that the left gaze bias they obtained was stronger at 6 seconds compared to 20 seconds face presentation. At 2 seconds I report a relationship between left perceptual bias and duration and number of leftward saccades. It is distinctly possible that this relationship would disappear with longer stimulus duration.

Therefore, a methodological limitation of this approach was to require 2000 milliseconds of exposure before recording a perceptual response. This is problematic to a clear interpretation of the question of whether the eye movements here analysed reflect a left fixation bias or not. It is possible that I continued to collect eye movement data after many subjects had (albeit internally) made their gender decision. However, my results when reporting eye movement behaviour earlier in the trial, at first fixation, seem to suggest strongly that there is a clear left bias. Indeed Mertens et al (1993) reported that their left field bias was stronger at 6 seconds compared to 20 seconds. Although the time differences compared to the present study are considerable, it is possible that I would obtain a clearer effect were I to allow free viewing of the stimuli and harvest only eye movement data made prior to gender decision. Indeed Phillips and David (1997) suggest that their failure to obtain a clear perceptual bias with their own stimuli was due to overexposure to the stimuli at 5 seconds duration which diluted any right hemisphere dominance. We shall return to this issue in chapter two.

As a caveat, the skew in terms of gender mix in the current study deserves some comment. A large study involving 144 subjects conducted by Luh, Redl & Levy (1994) reported no differences in the patterns of results obtained from men and women while testing gender and emotion decisions to chimeric stimuli. However, with regard to eye movement behaviour Mertens et al. (1993) reported that the left gaze bias for whole faces exposed for 6 seconds

was significantly stronger for females (19 male, 14 female). On the other hand, Phillips and David (1997) (who used happy-sad line drawings for 5 seconds and requested subjects to state whether the stimuli appeared happy or sad) reported no significant gender effects with regard to either perceptual decisions or eye movement behaviour. On balance, therefore, it would be advisable to employ equal cells to allow for gender difference comparisons.

As a conclusion to experiment 1, in an on-line eye movement monitoring task involving gender decisions to chimeric facial stimuli I report a strong perceptual bias to the left side of chimeric faces. Analysis of the eye movements of participants during the task revealed a subtle relationship between eye movements and perceptual responses. The first saccade made to chimeric stimuli was to the left in the vast majority of trials. In addition, for both the fixation duration and the number of fixations I found no overall leftward eye movement bias but a relationship between a left perceptual bias and the number and duration of leftward fixations.

Experiment 2: Does inversion abolish the left chimeric face processing advantage?

Introduction

It is now well established that upright faces are recognised more accurately and faster than inverted faces [the 'face inversion effect': Yin, 1969; Rhodes, 1993; Gauthier & Tarr, 1997, Cloutier, Mason & Macrae, 2005]. Cloutier et al (2005), for example, presented upright and inverted faces of famous and non famous faces and required participants to make either gender

(categorisation) or familiarity (identity) decisions. They reported that subjects were faster to make decisions to upright faces. Bindemann, Burton, Hooge, Jenkins & De Haan (2005) also reported that their subjects were slower to respond when upright faces were presented compared to inverted faces. Manipulations of presentation times led the authors to believe that upright faces not only capture attention more than other types of stimuli, including inverted faces, but also hold attention more. However, initiating interest in this phenomenon was the report of Yin (1969), that although all objects normally seen in one orientation are more difficult to remember when inverted, faces are especially so.

The importance of configuration

Sergent, in her influential 1984 paper, argued that faces have both component properties and configural properties that are related to relationships amongst features. Using multidimensional scaling analysis on manipulated face images, she examined the processes that underlie the seemingly unique nature of face processing, to explore how face processing relies on these kinds of properties. In her task subjects matched manipulated images presented both upright and inverted. She reported evidence that the relationships between various features of a given face were used in specifying the identity of the images presented, not just the use of individual features in an independent manner. She found some evidence that subjects do not rely on configural processing of the image when the face is inverted, and that thus different operations underlie the processing carried out on the two types of images, with inversion disrupting the extraction and processing of configural information.

More recently, Moscovitch, Winocur & Behrmann (1997) extensively tested patient CK, who has associative visual object agnosia, leaving him severely impaired in his ability to recognise objects yet apparently sparing his ability to recognise faces, and conclude that disruption to configural information is the key to the disruptive effect of inversion.

Expertise and configural processing

The recognition advantage for upright faces has also been attributed to 'expertise' with a homogeneous class of stimuli seen in one orientation in every day life (Diamond & Carey, 1986; Valentine, 1988).

Diamond and Carey (1986) examined the effects of inversion on images of faces and landscapes in a recognition test. Faces were found to be more vulnerable to inversion than landscapes. Diamond and Carey then proposed a relational properties hypothesis regarding how faces share the same configuration to explain this. They referred to first order relational properties as the points on a face that are common to all faces which would allow, for example, a set of corresponding points on several faces to be averaged and to produce a set of points which could in turn be recognised as a face. However, as the shape of a face (and other objects which share a common configuration) is constrained with regard to first order properties, they also, in turn, distinguish such first order relational properties from second order relational properties, which individuate faces, and refer to distinctive relations among the elements that define the common configuration. Diamond and Carey's celebrated third experiment demonstrated that expert dog handlers and breeders, but not novices, also showed an inversion decrement for photographs of dogs that was similar to the decrement for faces. They concluded that the expertise of the handlers allowed them to use the second

order relational properties of the images that individuate the dogs (like the faces), and that it is this individuation property of second order relational properties that is sensitive to inversion. Thus it is expertise that affords the ability to use second order relational properties that individuate members of a class that share a common configuration (through first order relational properties) that underlies the 'special' nature of face processing.

The role of expertise

Rhodes (1993) examined the role of expertise with regard to the use of configural processing in upright and inverted faces. Experiment 1 used Caucasian and Chinese subjects exposed to *same* and *other* race faces. Upright or inverted pairs of faces were shown bilaterally and identified from a choice array in the same orientation. She reported that the expected own race advantage for upright face recognition was only found in the Caucasian subjects. Expecting that the greater use of configural information due to expertise would be demonstrated by a larger inversion decrement for own race faces, she reported that Caucasian subjects showed a larger effect of inversion decrement for own race faces (additionally an inversion decrement for own race faces was demonstrated but was only marginally significant for Chinese subjects). Rhodes predicted that a left visual field recognition advantage would be larger for own race faces in the upright condition, a prediction that was not upheld.

Gauthier and Tarr (1997) devised a novel stimuli group named 'Greebles' to study the effect of expertise on sensitivity to changes in nonface stimuli. Greebles are three dimensional homogenous sets of nonface stimuli defined by a central body with 4 protruding parts. Changes to these four parts allow categorization at the individual, gender and family level. Over six

fMRI sessions, Gauthier, Tarr, Anderson, Skudlarski, & Gore (1999) reported that an upright advantage for Greebles was induced in their participants in a sequential matching task, complementing the advantage enjoyed by faces. This preference for upright Greebles was demonstrated by their participants following the development of expertise for these kind of stimuli. Moreover, the effect of the development of expertise appeared to be localised to the right hemisphere.

Models of configural information processing with face stimuli

Although broadly in agreement with the proposal of Diamond and Carey (1986) regarding first and second order features of configural processing, Rhodes and colleagues have developed a model which develops the argument along a different line. Rhodes (1988) referred to first order features as discrete features such as the eyes or mouth, which can be characterised independently. She referred to second order features as "configurational ones characterising the spatial relations between first order features, the position of first order features, and information about face shape". Thus the eyes are a first order feature, whilst the distance between the eyes is a second order feature. Again using multidimensional scaling analysis she reported that both types of features are encoded perceptually and used in face similarity judgements.

Rhodes, Brake & Atkinson (1993) also referred to second order features as relational features, and investigated the proposal that inversion disrupts the processing of these kinds of features more than first order features. They employed a recognition test where the target face had been adjusted in terms of isolated features or relational features and reported that inversion had a stronger impact on second order relational changes than first order changes.

They suggest that deviations of second order features from a facial 'norm' may be how such features are coded and used to differentiate a given individual face.

Holistic processing

Rossion and Gauthier (2002) point out that an important debate with regard to configurational processing relates to whether the processing is better described as relational, as outlined above, or holistic. Although Rhodes appears to advocate some degree of holistic processing in her configural norm comparison proposal, Tanaka, Farah and colleagues make a stronger case for holistic processing. Tanka and Farah (1993) argue that face processing is special as it involves relatively little or no decomposition into parts, but rather that the face is processed as a whole object.

Tanaka and Farah (1993) point out that the visual system may break an object like a house into parts such as doors and windows, which are explicitly represented as parts, which are then linked together to be ultimately represented as a house. By viewing the processing of a face as holistic, they see the difference lying in the fact that the face is not processed as a series of represented parts, but as a whole face, without an internal part structure, or at least more so as a whole object than other objects. They required subjects to learn upright faces and then identify isolated facial features from the images or identify the whole images compared with one with a changed feature (such as a different nose). Results showed that subjects performed better at identifying facial features when they were presented in the whole face than when those features are presented in isolation, a difference not seen with scrambled faces, inverted faces or houses. This was the case even though the whole face or the separate part condition had no difference in terms of

discriminating information. The authors argued that this suggested that whole faces were processed more holistically than other objects.

Farah, Tanaka & Drain (1995) suggest from this that the face inversion effect is therefore explainable from the use of holistic, non-part based representations for upright faces, whilst Farah, Wilson, Drain & Tanaka (1998) suggest that the concept of holistic representation is a continuum with faces processed most holistically, houses less so and words not at all.

Distinctiveness

With regard to the disruption to configural information in producing the inversion effect, Leder & Bruce (1998) examined the possible dimensions that contribute to the distinctiveness of a face and distinguished between relational aspects, such as the distance between the eyes, and local features, such as the thickness of eyebrows, and manipulated distinctiveness in faces by manipulating these two components separately from an original face image. Subjects were required to rate the distinctiveness of faces in either upright or inverted presentation. Results indicated that both of the manipulations increased the distinctiveness of the faces in the upright condition to an equal extent, but the distinctiveness effect of the relational manipulation was more reduced by inversion than the manipulation of local features. A follow up study using only internal features again indicated that distinctiveness ratings for both kinds of manipulation were higher for upright faces relative to normal control faces. In the inverted presentation the distinctiveness manipulation was only significant for local feature manipulation whilst relational manipulation no longer differed from the original unmodified images. Thus the manipulation of the local features still had an effect of distinctiveness in the inverted condition whilst the effect of manipulating the relational feature

distinctiveness disappeared. Thus they conclude that distinctiveness due to changes in relational aspects of the face was more reduced than distinctiveness effects due to local changes with inversion.

Inverted faces still hold some special significance

However, other evidence suggests that inverted faces still hold some special significance above other kinds of stimuli. Kanwisher, Tong & Nakayama (1998) measured fMRI responses in the fusiform face area (FFA) to both inverted and upright greyscale and Mooney faces (blobby, monochromatic face images that appear not unlike Rorschach ink blobs when inverted), postulating that inversion of a greyscale face impairs the ability to detect a face whilst inversion of a Mooney face actually impairs the ability to even detect a face. Subjects were required in one instance to merely view faces and in a second condition to match sequentially presented faces. For greyscale faces they reported a higher signal for upright compared to inverted faces. Of interest was the report that there was a trend to an interaction in the results, namely that lower response to inverted faces was seen in fewer subjects in the matching task than the passive viewing task. In addition, they reported that the response to inverted faces was stronger than that typically seen for non face objects. Also, the response for inverted faces during the matching task was just as strong a signal as it was to the response to upright faces in the passive viewing condition. Therefore they concluded that brain activity in the FFA was considerable to inverted faces in the matching task.

Lewis and Edmonds (2005) proposed that when searching for a face in an array that three stages are involved in a present/not present decision. A pre-attentive, or parallel processing stage which can guide attention to a location that may contain a face image. This stage can be affected by

luminance reversal but not inversion. The second and third stages can be affected by inversion and may include a rotation of the attended face region and a third stage involving template matching to the rotated image or a recognition process. They reported that faces popped out of arrays when searched for, indicating a parallel search, even when the target face was inverted in the array. The inverted faces finding indicates, they suggest, that it is not the special arrangement of features of a face when it is upright that provide pre-attentive guidance in detecting a face. A fourth experiment indicated that luminance reversal was found to change search from parallel to serial. This was not the case for inversion, which the authors suggest affects some process after the face has been located and attended in this particular search. Of interest to the conclusions of Kanwisher et al (1998) was a fifth experiment, which compared both simply detecting or recognising faces that were inverted or luminance reversed in the array. It was found that both inverting faces and reversing luminance had a larger effect on familiar faces than unfamiliar faces. The authors concluded that inversion affects face detection and has a further effect that is specific to face recognition. Therefore they propose that inversion has independent effects at two separate stages of face processing.

Sergent (1984) suggests that facial inversion causes a disruption of the ability to process a face's configurational aspects. Related to this, it has also been speculated that the right hemisphere has the advantage in holistic processing and the left hemisphere in part processing. This would mean that the right hemisphere employs holistic processing on the upright configuration of a face but that the inverted face destroys this normal configuration thus requiring the face to be assembled piecemeal, a task more efficiently carried out by the left hemisphere (McCarthy, Puce, Belger, & Allison, 1999).

Neuroimaging studies further suggest that face inversion may shift the focus of activation from face specific to object specific systems (Haxby et al, 1999; Aguirre, Singh, D'Esposito, 1999).

So taken together there is a strong suggestion that inverted faces are processed differently from upright ones, with some evidence that they may still hold a special significance in perception. In experiment 2 I examined whether subjects would use the information from the left side of the face to inform their gender decisions when upright chimeric male/female, female/male stimuli were presented, in line with previous research (Burt & Perrett, 1997; experiment 1 herein). Additionally, and more importantly I examined if this effect would not only be present for upright faces but also for inverted (flipped) faces.

Method

Participants

Twenty participants (10 female and 10 male, mean age 20.3, S.D.=1.3) took part in the study on a voluntary basis. They were all right handed as assessed by the Annett Handedness Inventory, and had normal or corrected to normal vision. Ethical approval was given by the University of Glasgow Ethics Board and all subjects gave written consent.

Procedure and Stimuli

Forty faces were used in the study: 10 pairs of male and female blended stimuli and 10 pairs of chimeric male/female and female/male stimuli. Stimuli were similar to the set described in experiment 1, (see Figure 1.1 for example), although reduced to 8 bit format to satisfy the requirements of the Experimental Run Time System (ERTS) software used to conduct the study

(Beringer, 2000). Chimeric and whole faces were presented on an IBM 17" computer screen with a participant chin rest situated at a distance of 57cm.

Four blocks of 40 trials of upright faces and four blocks of 40 trials of inverted faces were presented. The inverted faces were the same stimuli but flipped so that the left side remained the left side in each trial. After an initial fixation point the face was presented and the subject indicated the gender decision by pressing one of two response buttons located centrally in front of the subject (one above the other marked male and female). Response buttons were reversed for half the participants and face presentation was also counterbalanced in that half the participants saw the inverted faces first and then the upright faces and the other half vice versa.

Accuracy levels (percentage correct) for whole male and whole female faces were recorded for both upright and inverted faces. Male and female responses to chimeric faces were converted into left and right bias responses, again separately for upright and inverted faces.

Results

A paired sample t-test revealed a significant accuracy difference between the upright and inverted whole faces ($t(19) = 9.7$, $p < 0.05$) but, considering that faces were blended and thus androgynous looking, accuracy levels were high for both (85% and 74% respectively). Regarding response bias in relation to the chimeric faces, a paired sample t-test showed again that there was a significant difference between the bias for upright and inverted stimuli [$t(19) = 2.3$, $p<0.05$], in that the left perceptual bias was larger for upright (57%) than inverted faces (53%). Additionally, one sample t-tests against chance showed that the left bias for upright chimeric faces did differ

significantly from chance performance ($t(19) = 4.3$, $p < 0.05$) but the one for the inverted chimeric faces did not.

Inspection of the individual subject data revealed that two subjects showed chimeric face biases for upright faces with values more than 2 Standard Deviations away from the average mean. The mean perceptual bias for both subjects in question was 41%, whilst the perceptual bias range for the remaining 18 participants was 48% to 68% (with all but one participant above 50%). When these subjects were excluded from subsequent analyses I again found a significant accuracy difference between upright and inverted whole faces ($t(17) = 9.0$, $p < 0.05$) although again levels were high for both upright and inverted stimuli (86% and 74% respectively). Further the response bias in relation to the chimeric faces showed that there was a significant difference between the bias for upright and inverted stimuli [$t(17) = 2.6$, $p<0.05$] in that the left perceptual bias was again larger for upright (58%) than inverted faces (54%). This time, however, one sample t-tests against chance showed that the left bias for *both* upright *and* inverted faces differed significantly from chance performance ($t(17) = 7.4$, $p < 0.05$) and ($t(17) = 3.3$, $p < 0.05$) respectively (see Figure 2.1).

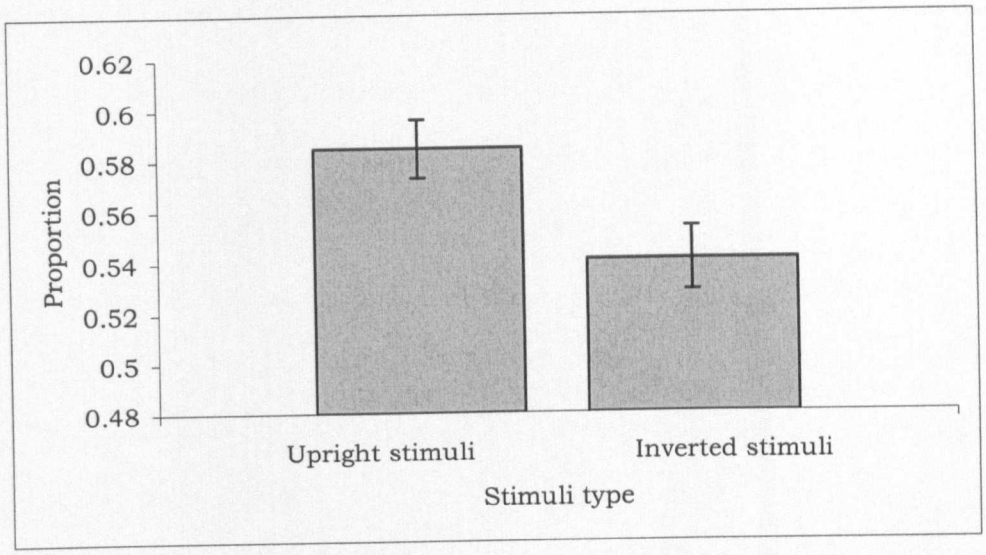


Figure 2.1: Leftward chimeric face bias for upright and inverted faces (after deletion of two subjects) indicating SE mean error bars

Discussion

Using subtly blended chimeric images I report clear evidence that subjects used the information from the left side of the face to inform their gender decisions. This result replicates the gender effect obtained with similar stimuli by Burt & Perrett (1997) and previously herein with experiment 1. It is also in line with other findings of a left perceptual bias for gender, age, attractiveness and emotion cited previously (Burt & Perrett, 1997; Schyns, Bonnar, & Gosselin, 2002; Luh Rueckert, & Levy, 1991; David, 1993).

Most interestingly though I found that this chimeric face bias was not abolished when the faces were flipped (inverted). Once the experimental outliers were removed, significant leftward face biases were found for both the upright and inverted faces although, as expected, the biases were significantly larger for the upright faces. In line with this, subjects also produced high accuracy scores on the inverted faces although again, as expected, judgements of upright faces were significantly more accurate (see Moscovitch, Winocur, & Behrmann, 1997, and Bauml, Schnelzer, & Zimmer, 1997 for similar effects).

I would propose that both the accuracy and chimeric bias effects found here argue against the idea that inversion destroys the right hemisphere superiority for faces (McCarthy, Puce, Belger, & Allison, 1999). If this was indeed the case, flipping the chimeric faces should have resulted in a loss of the left face bias. This was, however, not the case although the effect was reduced.

This then begs the question, as to what is driving this (albeit reduced) effect? The subjects were clearly not guessing, as indicated by the accuracy levels obtained for single gender stimuli. They were also more likely to base their decision on the gender information available to the left side of the image.

Faces can be processed (configurally or otherwise), to a number of different ends, i.e. recognition, determination of age, determination of emotional state and so on. The task in the present study was a simple determination of gender. Some time ago Fellous (1997) reported that only 5 measures (distance between the outermost corners of the eyes, distance between the cheek bones, width of the nose, distance between the eyes and the eyebrows and distance between the eyes and the mouth), could accurately predict the gender of 57 faces in his test set. Accuracy was considerable, at 87.1% for males, and 92.3% for females. All 5 measures used were either horizontal or vertical measures. Thus although inversion disrupts our ability to take advantage of configurational information, it may be possible that the subjects developed a strategy that consciously employed some simple form of configurational judgement to aid their decisions. Such a strategy may in turn have led the subjects to display a right hemispheric, and hence leftward bias.

Cloutier et al (2005) reported that although reaction times for both judgements of sex and identity were affected by the orientation of the face it was found that the cost was more profound for judgements of identity (familiarity) than for sex. For errors, although more errors were made for

inverted faces, more errors were made overall for identity than sex decisions. Furthermore, an interaction revealed that only identity decisions were affected (in terms of accuracy) by inversion with no effect on sex judgements. Arguing that sex decisions can be made on the basis of even a single feature, they conclude that compared with configural extraction, the extraction of feature based information is less dependant on the orientation of the image, thus, that it is easier for the face processing system to extract categorical than featural information.

Conversely, Brown & Perrett (1993) reported that facial features can convey gender information alone or with regard to their configuration, and that gender information is not exclusively carried configurally. When viewed in isolation they found, for example, that the brows and eyes carried the most gender information in their study, whilst when viewed in the context of other (opposite sex) features it was reported that the jaw had the strongest influence on gender selection. Their data thus implies that single features can convey gender information, and it is possible that my subjects were able to extract meaningful gender information from a single feature viewed in isolation. Identifying the gender of an inverted face is, even intuitively, more difficult that determining the gender of an upright face. Therefore my subjects may have adopted a strategy of focusing on a particular feature which carried gender information in order to simplify the task.

This latter explanation requires the assumption that the subjects preferentially viewed the left features. In fact in line with this argument, in experiment 1 I have reported that a significant proportion of initial saccades made to these chimeric stimuli were to the left side of the face. Moreover, using the so called 'Bubbles' technique, Schyns et al (2002) reported a

complementary finding of left lateralisation for face processing in gender identification tasks, implicating processing of the left eye in particular.

Therefore in conclusion experiment 2 reports that the left processing bias apparent in chimeric faces is not abolished when the face is inverted, although it is reduced. It would appear that this finding does not support the idea that inversion destroys the right hemisphere superiority for faces.

Chapter 2

Experiment 3: Can eye movement patterns explain all perceptual biases in chimeric face processing?

Introduction

Recently, Ferber and Murray (2005) published a prism adaptation study disputing any clear link between chimeric face bias and eye-movement patterns: although they found a left eye-movement bias with a left chimeric face bias, when eye-movements were shifted to the right (using prism adaptation), they failed to observe a concurrent shift in the chimeric face judgements. From this finding, the authors argue that overt motor responses such as eye-movements are not required in order to produce perceptual biases in chimeric face judgements.

Following their argument, if we were to exclude eye movements completely from the behaviour of our subjects, the perceptual bias should still be present. Interestingly, Grega, Sackeim, Sanchez, Cohen, & Hough, (1988) were able to obtain a significant perceptual bias with stimuli with an exposure duration of only 1 second. However, this interval still allows participants to make several saccades during stimulus exposure. More relevant are the findings of David (1993), who employed stimuli that required an *emotional judgement*, and reported a left field perceptual bias with chimeric face *drawings* exposed for 120 milliseconds. In the present study I turn to investigate whether a reliable left perceptual bias can be demonstrated employing the *realistic* face stimuli used in the previous two experiments but,

like David's study, presented below the threshold of eye-movements and requiring a *gender judgement.*

Method

Participants

Seventeen right-handed participants (10 female and 7 male, mean age 21, S.D.=2.1) took part in the study. All gave informed written consent and procedures were approved by the Glasgow University Ethics Review Board.

Materials and stimuli

Stimuli and equipment were as in experiment 2 (upright condition). A response pad was situated on the subject's mid-sagital axis with two keys aligned in a vertical position. Responses were made with the right hand only. Positioning of male and female response labels was counterbalanced between participants and the distance between the computer screen and the chin rest was 57cm. Five blocks of the 40 faces were presented and each face was preceded by a blank screen for 195 milliseconds, followed by fixation cross presented for 2000 milliseconds, followed by a blank screen for 195 milliseconds. Each facial stimulus was then presented for 100 milliseconds followed by a blank screen. Following presentation of the face image, subjects were asked to indicate the gender by pressing one of the two keys. Participants were allowed a maximum window of 2500 milliseconds to make a response, at which time the trial would time out and the next trial would commence.

Results

Accuracy

Of the whole faces 26% of male and 18% of female faces were incorrectly identified. This was again expected as the stimuli were androgynous looking faces as previously stated, and in addition, presented very briefly. A paired sample t-test of male and female accuracy indicated no significant difference ($t(16)=1.94$, $p=0.07$).

Perceptual bias

Interestingly, information on the left hand side of the face again dominated the gender decisions in that 55% of responses were based on the left side of the chimeric face ($t(16)=3.56$, $P<0.01$). However, although still significant, the size of this effect was reduced considerably compared to experiment 1 (63%). An independent samples t-test indicated that the level of bias was significantly different between experiments 1 and 3; $t(35)=3.059$, $p<0.01$ (two tailed).

Discussion

Thus results thus show that even with a very brief exposure duration, that should not allow any eye-movements, it is still possible to obtain a significant left perceptual bias with *gender based* chimeric images. These findings of a perceptual bias at short presentation times are in line with David (1993). Moreover, the results can be taken as support for Ferber and Murray (2005), and also older studies by Grega et al. (1988) and Phillips & David (1997) who failed to find a link between eye-movement patterns and chimeric

face biases. In addition though the present results also show that this bias is significantly stronger when eye-movements are possible.

In previous studies various forms of chimeric images have been employed to elicit perceptual biases, including spliced photographs, cartoon images or line drawn tracings. This may be warranted, as Ishai, Schmidt, Boesiger (2005) reported that in their fMRI study that there was no difference in activation between line drawings and photographs of unfamiliar faces, although the two types of stimuli were not processed with equal levels of efficiency (Leder, 1999). However, Luh, Reuckert & Levy (1991) suggest that if line drawings are over-simple then subjects can rely on simple decisions regarding an upturned or downturned mouth arc to make their emotion decision, for example.

The stimuli employed in the present study were originally designed by Burt & Perrett (1997) to be as realistic as possible. Burt and Perrett argued that if subjects are aware that the stimuli are chimeric they may not engage normal face processing mechanisms. Therefore, to ensure that results are indicative of cognitive processes relating to face perception, and hence as ecologically valid as possible, it is desirable that stimuli should not cause subjects to engage in unwanted or possibly confounding extraneous cognitive processes.

Indeed Hoptman & Levy (1988) examined the issue of the use of photographic and cartoon chimeric face images in generating lateral biases, and concluded that although both stimuli have a considerable overlap in the statistical variance they produce, a component of the variance is unique to either task, indicating a possible difference in the underlying functions they reflect. Moreover, Luh, Rueckert & Levy (1991) conducted chimeric faces tests with both photographic and cartoon versions of emotional and gender based

chimeric faces and found that the source of reliable variance around the mean for the photographic emotion task had more in common with the gender photographic task than with the emotion based cartoon task, and similarly the emotion cartoon task had more in common with the gender cartoon than with the emotion photograph task.

The present study makes two important points in relation to this; firstly that the results have been obtained using stimuli with a high degree of ecological validity, thus ensuring a high likelihood that participants will engage in normal face processing mechanisms. Secondly, the results permit a direct comparison of performance between two equivalent subject groups, those studied previously in experiment 1 who were allowed eye movements and the present group who were not, with similar facial stimuli.

Contextually, the results are viewed within the framework of the Bruce & Young (1986) and Haxby, Hoffman, & Gobbini (2000,2002) models of face processing. Haxby and colleagues draw on the influential model of Bruce & Young to propose a neurological model of face processing that is based on a core system and an extended system, and they take the view that recognition of the identity of a face can be dissociated from the perception of gaze or facial expression and there is a strong body of imaging evidence to support this theory (e.g. Phillips et al, 1998; Streit et al, 1999; Hoffman & Haxby, 2000; Ishai, Schmidt, Boesiger, 2005).

In the Bruce & Young (1986) model the identification of semantic information such as gender is argued to be independent of face identification per se, and is processed in parallel. Indeed gender may be processed more expediently as Cloutier, Mason & Macrae (2005) reported that when limited time is allowed, gender decisions to faces can be made more quickly than identification decisions. However, suggesting a modification to the Bruce &

Young (1986) model, Rossion (2002) proposes an account of the cognitive processes involved in face processing in which either overlapping or even identical perceptual information is extracted when gender or identity judgements are made. Related to this, Bülthoff & Newell (2004) provide evidence that with regard to faces, a person's gender is related to their identity, whilst expression is unrelated, also arguing for a revision to the Bruce & Young model to account for this. Similar evidence is provided by Ganel and Goshen-Gottstein (2002).

In line with this, a difference in performance between gender and emotion based chimeric faces tasks has been reported for Schizophrenic patients by Gooding & Tallent (2002). They argue (in line with Haxby et al. 2000, 2002) that relative to the processing of facial stimuli in general, the processing of emotional faces uses additional resources, and that such patients may have a difficulty that is demonstrated at the emotional extraction stage, as they did not differ from controls on a gender based chimeric faces task.

It is therefore argued that perceptual biases obtained from chimeric stimuli employing *gender* may reflect processes that lie closer to true face processing mechanisms than those employing an *emotional* judgement. In fact several studies have reported that perceptual biases are stronger for emotional decisions to chimeric faces compared to gender decisions (Gooding & Tallent, 2002; Compton, Fisher, Koenig, McKeown & Muñoz, 2003). Luh, Rueckert & Levy (1991) suggest that an emotion component in a chimeric faces task augments a right hemisphere involvement in face processing tasks.

Several researchers advocate a position that emotion processing is right lateralised in the brain (Christman & Hackworth, 1993; Ashwin, Wheelwright & Baron-Cohen, 2005; Borod et al 1998; Kucharska-Pietura, Phillips, Gernard

& David, 2003). Although it has to be said that is argument is controversial, with other researchers advocating the valence hypothesis, a position whereby each hemisphere has a realm of dominance for particular emotions (Reuter-Lorenz & Davidson, 1981; Reuter-Lorenz, Givis & Moscovitch, 1983; Jansari, Tranel & Adolphs, 2000; Nicholls, Ellis, Clement & Yoshino, 2004; Canli, Desmond, Zhao, Glover & Gabrieli, 1998; Graham & Cabeza, 2001; van Strien & van Beek, 2000; Rodway, Wright & Hardie, 2003; Moretti, Charlton & Taylor, 1996; Asthana & Mandal, 2001). Therefore considerable data exists indicating some form of emotional lateralisation, thus supporting the present account that an emotional task component may provide an additional bias.

An additional advantage of employing chimeric images without emotional content, aside from their own potential laterality, lies in the reports that the emotional state of the subject can have an impact on the perceptual laterality of chimeric faces employing emotion (Heller, Etienne & Miller, 1995; Jaeger, Borod & Peselow, 1987). Moretti, Charlton & Taylor (1996) reported differential emotional decisions to sad faces in depressed compared to non-depressed subjects, whilst Compton, Fisher, Koenig, McKeown & Muñoz (2003) reported that women's responses to a depression questionnaire are related to their scores on an *emotion* based chimeric faces task but not a *gender* based one.

Therefore, in conclusion, what is striking about the data in experiment 3 is the fact that despite using the same *gender* based chimeric face stimuli, the effect of the perceptual bias reported here was much reduced compared to experiment 1, which monitored eye-movements. With brief presentation times experiment 3 obtained a significant perceptual bias effect employing decisions to chimeric faces regarding gender. This demonstrates that a chimeric face bias can indeed be elicited without eye-movement but that eye-movements

enhance the effect. This suggests that when a preferred scanning direction can be deployed in this type of facial judgement task, such a deployment will preferentially increase the salience of left hemi-field stimuli, leading to increased perceptual biases to this side of space. If this is the case then a systematic increase in face presentation time (thus allowing a systematic increase in eye-movements) should systematically increase the perceptual bias effect. This issue will in turn be addressed in experiment 4.

Experiment 4: What are the effects of aging and exposure duration on perceptual biases in chimeric face processing?

Introduction

Experiment 3 indicated that it is possible to obtain a significant perceptual bias with chimeric facial stimuli presented at sub-saccadic exposure thresholds. However, the degree of bias was clearly reduced by a statistically significant degree. I have thus concluded that when exposure duration is significantly long to allow a preferred scanning direction to be employed, such a preferred scanning direction will be employed, preferentially enhancing the salience of the left visual field of the stimulus, thus leading to an increase in perceptual bias to stimuli presented to the left visual field. I have proposed that a systematic increase in exposure duration should thus systematically increase the perceptual bias effect. If evidence from experiment 3 is reliable, a successful replication, in terms of a significant perceptual bias at 100msec, should be demonstrable, however the evidence from experiment 1 also indicates that we should obtain a significantly higher degree of perceptual

bias if the stimuli is presented long enough to obtain meaningful eye movement behaviour (i.e. if the participant can make saccades over the image). Thus in the present study I shall turn to address the influence of variable presentation durations, in order to examine the proposed modulation this will have on the degree of leftward perceptual biases obtained from exposure to chimeric face stimuli.

Additionally the paradigm to be employed in the present study lends itself well to addressing a further issue in face processing I have not yet addressed, that of the effect of healthy aging on face perception per se, and on perceptual biases to chimeric faces in particular.

Healthy aging and face perception

It is extremely valuable to have a comparison between the performance of a younger and an older age group of subjects with the same stimuli, as there is converging evidence that the performance of the two groups will not be the same, in tasks tapping into multiple cognitive processes. As I have hopefully demonstrated by now, there is considerable evidence that face processing is a right hemisphere activity. However, there is also converging evidence that tasks that selectively engage the right hemisphere may be executed in a different fashion in an elderly compared to a younger sample of subjects. Older adults have been reported to display differing levels of performance, both in terms of accuracy and latency, in a broad spectrum of domains.

Age related task differences: functional imaging

Daselaar, Veltman, Rombouts, Raaijmakers and Jonker (2003) used fMRI to examine behavioural and brain activation responses in younger and

older adults undertaking a deep and a shallow classification task with lexical stimuli. Behavioural data indicated equivalent levels of latency and accuracy between the two groups. Imaging data revealed a great deal of functional overlap between the two groups, however, comparing deep versus shallow encoding indicated that the younger group demonstrated an increase in left hippocampal activity whilst this was not the case for the older group, indicating that brain activity patterns were not identical between the groups. Grady et al (1995) also reported differences in functional activation during PET scanning of older and younger groups in a face encoding and recognition task, including differential patterns of interaction between the hippocampus and cortical areas between the two groups during encoding.

Grady et al (1994) conducted a PET study of older and younger adults, which included face-matching conditions. They reported considerable differences in areas of either increased, or diminished, activation between the two groups during the task. Although demonstrating areas of reduced functioning in several cortical areas, older adults also displayed greater bilateral activation in the fusiform gyrus, inferior frontal gyri and dorsolateral prefrontal cortex.

There is further evidence that the aging process does not involve diffuse or global changes to the brain, but that in many domains it involves specific and selective changes. Lawrence, Myerson and Hale (1998) used verbal and visuospatial tasks with various age groups and reported a far greater slowing with age of visuospatial abilities, regardless of the fact that both types of tasks required speeded responses. Klisz (1978) noted that the scores of older people in psychological assessments decline, but are not as severe as declines seen in individuals with brain damage. Further, she noted that the performance of older adults does not resemble the performance of those with left sided brain

damage, but does resemble that of the performance of those with damage to the right side of the brain. Klisz took this as evidence that left hemisphere functions are better maintained in the face of the aging process, whilst functions of the right hemisphere are more sensitive to aging.

The right hemisphere, or Differential Aging Hypothesis

Goldstein and Shelly (1981), studying a large, multiple age group population of medical and neuropsychiatric patients with a neuropsychological test battery, reported an increase in dysfunction of the right hemisphere with age, although they also reported evidence for a less robust pattern of results for the left hemisphere in the same direction. This theoretical point of view has been latterly described as the Differential Ageing Hypothesis.

Evidence from other sources has supported the findings of Goldstein and Shelly (1981). Meudell and Greenhalgh (1987) tested teenagers and over 60's with the AH4 Intelligence test. Even though both parts involved time limits, they reported that older adults showed poorer performance on the visuospatial part, the aspect of the test which was likely to be mediated by the right hemisphere, than on the verbal part compared, to the younger group.

Additionally, Gerhardstein, Peterson and Rapcsak (1998) interpreted their results as providing evidence for an age related decline in right hemisphere functioning. They exposed younger and older adults to line drawings of exemplars of objects, presented to one visual hemifield, in a same-different paradigm where the second drawing was in some cases rotated. With regard to hemispheric sensitivity, results indicated no effect of hemisphere for younger subjects, whilst older adults demonstrated evidence of greater sensitivity in the left hemisphere compared to the right.

Recently, Failla, Sheppard & Bradshaw (2003) demonstrated an effect of pseudoneglect in a line bisection task, where subjects have to mark a subjective centre to a line drawn on paper in font of them. They reported that the effect was present in subjects in a group with ages from 20-30, but was not present in a group with ages from 60-70. This lack of an effect of pseudoneglect was put down to either callosal degeneration or selective degeneration of the right hemisphere.

Equivocal evidence for selective right hemisphere aging?

In consideration of more specific age related changes in the brain, one theory that has attracted considerable research and discussion pertains to the view that the right hemisphere may in fact be more sensitive to the aging process. McDowell, Harrison and Demaree (1994) conducted a study with older and younger adults who were required to identify positive, negative and neutral emotional faces. Mixed support for selective right hemisphere aging was reported. Findings revealed that overall the younger subjects were more accurate, but that older adults were equally accurate for positive affect but impaired for negative and neutral affective facial expressions. Such a finding, if a lateralised benefit for valence processing is accepted, is very much in keeping with selective right hemisphere deterioration in older adults. However, less support was found in the second experiment using tachistoscopic, and lateralised, exposures of the same stimuli. This revealed that the older adults performance was in keeping with a valence hypothesis, with faster responses to angry faces in the left visual field and the opposite pattern for happy faces. However, less support for selective right hemisphere aging was found in the report of increased processing time for angry faces in the older adult group when such facial stimuli were presented to the right

visual field (thus the positive emotion dominant left hemisphere according to the valence hypothesis).

Sullivan and Ruffman (2004), interested in whether age related changes were related to general cognitive decline or specifically to a face processing impairment, conducted a number of studies examining age related changes in face and emotion processing between a young group and an older adult group. Initial results indicated that the older group was significantly more impaired on an emotion task than the younger group. Examining performance on specific emotions indicated that the older group was impaired at identification of sadness and anger. Study 2 involved a larger array of tasks involving two image comparisons of blended emotions where the subject had to specify which of the two faces conveyed more of a given emotion, two image comparisons of faces with blended genders, where subjects had to specify which face was more male, and a quantification task involving two images of glass beakers. Analysis of the results comparing the two groups indicated that the older group performed equally well on the latter two tasks but was more impaired on the emotion task relative to the beaker task, when compared to the young group. By conducting analysis co-varying for basic gender task performance the study also reported that the older adults were more impaired on the emotion task than the beaker task. Thus they conclude that the older adult groups difficulty with the emotion task was a difficulty that went beyond more basic face processing skills.

Reviewing the literature on emotion recognition deficits in the elderly, they report that the deficits appear to affect some emotions, such as anger and sadness more than happiness and surprise. They suggest from this review that the evidence for selective right hemisphere aging, taking account of the valence model of emotional processing, is mixed, as although the older adults

are more impaired in some negative (right hemisphere based) emotions, they are not particularly impaired on disgust which would be predicted by this interpretation. They suggest rather that their data is indicative of deficits in certain emotions being related to accelerated rates of age related degradation in areas such as the temporal lobes, amygdala and orbito-frontal cortex which are more closely involved in the processing of those particular emotions.

Finally, Moreno, Borod, Welkowitz and Alpert (1990) proposed that older adults, when compared to younger adults, should demonstrate a decrease in facial lateralisation of generated facial expression as several studies have proposed that facial expressions tend to be more strongly portrayed on the left side of the emitters face (see Borod, Bloom, Brickman, Nakhutina and Curko (2002) for a review), being more dominated by the emitters right hemisphere. Moreno and colleagues gathered ratings of emotional intensity during posed facial expressions of older, middle aged and younger adult posers conveying a range of emotional expressions. Results indicated that subjects of all age groups emitted facial expressions of emotion more intensely on the left hemiface.

The HAROLD model

Cabeza (2002) has proposed an alternative account of the effect of the aging process on the brain, the Hemispheric Asymmetry Reduction in Older Adults (HAROLD) model. The model primarily hypothesises that prefrontal cortex activity in older adults becomes less lateralised, possibly due to a combination of reduction in cognitive resources, cognitive speed, or a reduction in inhibitory control in older adults.

The model primarily draws on neuroimaging evidence from memory, perception and inhibitory control for support. For example, Madden et al

(1999) reported age-related differences in a PET study with young and older adult groups in a memory study employing word stimuli. The study reported age related differences in thalamic activity, both in encoding and retrieval. Additionally, analysis indicated age related increases in prefrontal activity in retrieval, with younger adults showing activation primarily in right prefrontal cortex, whilst older adults displayed bilateral activation of prefrontal cortex.

The model is particularly distinguished from selective right hemisphere aging by also encompassing situations were older adults may display increased left or right hemispheric activity compared to younger adults in tasks that tend to be more lateralised in younger adults. Cabeza (2002) suggests the roots of the model can be explained by both compensatory mechanisms or a developmental age related difficulty in employing specialised neural modules (dedifferentiation) or possibly both. Such age related changes could be argued to stem, reports Cabeza, from either changes in cognitive architecture (a psychogenic view) reflecting altered cognitive strategies, or reflect an actual change in neural architecture.

Support for the HAROLD model

Several recent studies have published results in line with Cabeza's hypothesis. Grady, Bernstein, Beig and Siegenthaler (2002) employed PET scanning in younger and older adults in an encoding and recognition task employing facial stimuli and found evidence of bilaterality of working memory in older adults compared to younger adults. Behavioural results indicated that the older adults displayed poorer face recognition, regardless of the type of encoding employed. PET results indicated different activity for the two groups, with one notable finding being a report of a positive correlation with

behaviour in young subjects in left prefrontal and temporoparietal areas which was found to be bilateral for older subjects.

Grady (2002) reports that a consistent finding in memory related face processing is often the greater activation of left prefrontal cortex in older adults compared to younger adults. Combining data from three previous PET studies involving face matching, face memory or degraded face matching she again examined age related differences. Initial imaging conclusions were that characteristic brain activity patterns showed no age related differences in face processing in general, suggesting that the brain mechanisms for face processing are generally unaffected by age, with activity noted bilaterally in both the fusiform gyrus and frontal lobes. However, in terms of signature brain activity when the different face processing tasks were compared, patterns were found that differentially characterised the younger group and the older group. These included increased prefrontal activity in the older group in degraded face matching compared to non degraded face matching. This was taken to be indicative of an earlier response to cognitive effort in the older group. Furthermore, differential correlations between latency and brain activity in the memory tasks in left prefrontal cortex and bilateral occipitotemporal regions were found between the two age groups. Grady concluded that prefrontal activity is task specific in face processing in younger adults, whilst in older subjects it appears to be related to tasks that are more demanding, independent of what the actual task requires the subject to do, and thus that prefrontal regions, particularly left hemispheric are relevant in discriminating age related differences in cognitive function.

Gunning-Dixon et al (2003) employed fMRI with younger and older adults to examine age related differences in cortical and subcortical activation during the processing of emotional faces, and their findings have merit with

regard to the HAROLD model. Stimuli were posed faces of positive, negative and neutral emotional displays (not examined separately) and subjects had to either define the emotion as either positive or negative or make an age judgement on the face. Results indicated that younger subjects were faster for both tasks and more accurate at the emotion task. Imaging data indicated the two groups actually showed activation in different cortical networks when processing the emotions, notably activation in the right amygdala for younger adults and greater activation in prefrontal regions in the older adults. Gunning-Dixon et al interpreted their results in terms of an age related reorganisation of cortical networks for emotional discrimination of faces.

Chaby, George, Renault and Fiori (2003) examined behavioural and ERP responses to detection of small changes to personally known and recently met faces in younger and middle aged adults. ERP responses were examined both with regard to the N170 component, reflecting the early visual stage of encoding, and the N2b and P3b components, related to stimulus categorisation and response choices. Behavioural results indicated no differences in accuracy or latency between the two groups. However, although both groups demonstrated an occipitotemporal N170 response followed by a frontocentral N2b and parietal P3B, distinct differences were observed in the nature of the ERP results. N170 amplitude was significantly greater for the middle-aged group. Also, N170 was found to be larger on the right than on the left in the younger group. N2b amplitude appeared to have a central peak in one central electrode in the younger group but was more evenly spread and verged to the left in the middle-aged group. Further differences were found with regard to the P3b amplitude response, namely that, although centrally peaking in both groups, the distribution over electrodes differed between the two groups with the response more evenly spread over electrodes in the middle

aged group and also spreading to the left in this group. Results were interpreted in terms of either compensation or changes in strategy to the task in the middle-aged group, and were also taken to correspond to a reduction in asymmetry.

A question addressed by Cabeza (2002) was whether such reductions in lateralisation reflect changes in the entire cognitive network that are related to a given cognitive process, or are limited to specific brain areas that actually display the effect. Cabeza concludes that although many age related changes in activity appear to be specific for a given task, there is also evidence that aging affects one hemisphere of the brain more than the other, and that both processes could be taking place.

Comparing the HAROLD and Differential Aging Hypotheses

Hausmann, Güntürkün and Corballis (2003) studied younger and older male and female groups in word matching, figural comparison and face recognition tasks in order to investigate whether the HAROLD or the selective right hemisphere aging model best fit the results obtained. Their main conclusion was that neither hypothesis was supported completely, and that different types of task can produce different results. Additionally, they report that age related changes in hemispheric asymmetry appeared to be related to gender in their study. With regard to aging, the face recognition task indicated only that the older group was less accurate, but results from the other two tasks revealed findings related to either hypothesis. In word matching they reported more left hemispheric dominance in the older group, in so far that a decrease in performance related to the right hemisphere was more marked in the older group, this is consistent of the prediction of selective right hemisphere aging and inconsistent with HAROLD. In the figural comparison

task there were effects of age that were modulated by gender, indicating, for example, that latencies increased for both hemifields with age for males, but increased in the right hemifield (left hemisphere) only with age in females. Additionally, left visual field (right hemisphere) advantages were reported for older women and younger men only. The finding of less lateralisation in older men is in keeping with HAROLD whilst the data of the older women does not fit and was indicative of poorer left hemispheric performance, which is counter to the predictions held for a hypothesis of selective right hemispheric aging.

As Dolcos, Rice and Cabeza (2002) suggest, it is possible that the contradictory evidence for differential aging of the right hemisphere may have its origins in the different methodologies applied to investigate it. It is also possible that selective right hemisphere aging does not apply in an absolute manner to all structures located in the right hemisphere. The evidence for HAROLD pertains primarily to the functional imaging literature, and cannot absolutely determine whether age related changes are due to changes in functional recruitment patterns or actually reflect structural changes. Dolcos et al suggest that the HAROLD and right hemispheric aging proposals do not necessarily have to be completely mutually exclusive. They point out that the latter attempts to explain changes in the entire brain, whilst the former primarily addresses changes in prefrontal cortex. Thus a plausible theory could dictate that the aging process results in differing patterns of hemispheric asymmetry. The prefrontal cortex may display a reduction in asymmetry as dictated by the HAROLD model, and areas such as the occipital and temporal lobes may display a pattern as we age which is more in keeping with the right hemisphere aging theory.

Chimeric face perceptual biases in relation to the aging process

The preceding pages have highlighted several age related differences in face processing, either within or outwith the context of the HAROLD or Differential Aging models, highlighting that in many cases older adults perform differently in face processing tasks in terms of functional activation (Nakamura et al, 2001), recognition accuracy (Grady, Bernstein, Beig & Siegenthaler, 2002) or emotional identification accuracy (Gunning-Dixon et al, 2003). Evidence for right hemisphere dysfunction in paradigms involving chimeric faces has not been strong however.

Levine and Levy (1986) conducted a free vision smiling-neutral chimeric faces task with multiple age groups. They reported significant leftward perceptual biases across all groups, and reported no evidence of an effect of aging with the older adults on the degree of left perceptual bias obtained, although there was some evidence of an impact of age with the very youngest kindergarten group. Such findings are clearly not in keeping with a hypothesis of selective right hemisphere aging.

Moreno, Borod, Welkowitz and Alpert (1990) proposed that older adults, when compared to younger adults, would display reduced perceptual biases to free view chimeric stimuli. Moreno and colleagues results indicated no age related difference in the degree of left perceptual bias in the chimeric faces test.

More recently, Cherry, Hellige and McDowd (1995) also exposed older and younger adults to a free vision happy-neutral chimeric faces task and reported that both groups displayed a significant left perceptual bias, and found that although the older adults did display a smaller perceptual bias, that this difference was not statistically significant. They concluded therefore that their results were not supportive of a right hemisphere ageing hypothesis

that would predict a decrease in left perceptual bias as people age due to an age related decrease in right hemisphere dominance for faces.

Finally though, Failla, Sheppard and Bradshaw (2003) conducted a free view chimeric faces task with happy-neutral stimuli with participants ranging in age from 5 to 70. They reported that all groups with exception to the oldest (60-70 years old) group displayed a significant left bias in the task, which the authors related to possible reductions in function of the right hemisphere.

The present study

Therefore the evidence is currently not too strong that chimeric face studies can further elucidate possible age related changes in performance in this right hemisphere dominant task as only Failla et al (2003) reported a statistically significant result. It is of note that all four studies cited employed spliced photographs, which, as reported in experiment 1, may not properly ensure that participants engage in normal face perception mechanisms. Therefore the present study seeks to further explore age related changes in perceptual biases in this right hemisphere task with the more lifelike stimuli employed in experiments 1-3.

The design of the study featured three exposure durations, one at a sub-saccadic 100msec and one of free viewing (as employed in the above four papers), additionally a third exposure duration of 300msec was employed. It was expected, if my view was correct, that the degree of bias should be significantly higher for the free view condition than for the sub-saccadic condition. I made no explicit prediction with regard to the 300msec condition but anticipated that the degree of perceptual bias should lie between the degree of bias obtained in the shorter and longer durations.

With regard to the effect of healthy aging on perceptual biases, both the HAROLD and Differential Aging Hypotheses accommodate a reduction in right hemisphere dominance for this task for older adults relative to younger adults. However, given the equivocal nature of evidence for reductions in perceptual bias reported to date, no specific predictions are made, although it is anticipated that the more realistic images employed should reflect a truer account of the perceptual processes at work in chimerical face processing with regard to the aging process.

Method

Participants

24 (12 male) young adults and 23 (9 male) healthy elderly volunteers took part in the study. The data of 2 male young adult subjects was excluded from the study as they failed to match the accuracy criterion (outlined below), so the average age of the 22 included subjects in the young adults group was 22.1 (SD 2.3). The data of 9 older adults was excluded from the study (1 male subject for left handedness, 1 male subject for failure to follow task instructions, and 7 subjects for failing accuracy criterion (4 males)). So the average age of the included older adults was 72.3 (SD 3.9). Thus 22 younger adults and 14 older adults were included in the study. All participants gave informed written consent and procedures were approved by the Glasgow University Ethics Review Board. All included subjects were right handed as assessed by the Oldfield handedness inventory.

Materials and stimuli

Except were outlined below all other aspects of the study were conducted as in experiment 3.

All participants were exposed to three experimental conditions in a counterbalanced order.

- 100msec condition: 4 blocks of the 40 faces were presented. Each face was preceded by a blank screen for 195 milliseconds, followed by a fixation cross presented for 2000 milliseconds, followed by a blank screen for 195 milliseconds. Each facial stimulus was then presented for 100 milliseconds followed by a blank screen. Following presentation of the face image, subjects were asked to indicate the gender by pressing one of the two keys. Participants were allowed a maximum window of 5000 milliseconds to make a response, at which time the trial would time out and the next trial would commence. Self paced rests were allowed after a block of 40 trials and between conditions.

- 300msec condition: As above, with the exception that facial stimuli were exposed for 300msec.

- Free view condition: As above, with the exception that stimuli remained on the screen until a response was made, with no time-out.

Results

Accuracy

Due to the brief presentation conditions involved, to ensure reliability of data, a strict inclusion criterion was applied: namely that participants were excluded from analysis if their accuracy was below 50% for male or female single gender faces in any of the three conditions. Proportional accuracy levels

for subjects in both groups included in the analysis, for single gender stimuli, in the three presentation conditions, can be seen in tables 4.1, 4.2 and 4.3.

Table 4.1: Mean proportion of correctly identified single gender stimuli for older and younger adults, and for both genders of stimuli.

Group	Mean accuracy	Stimulus type	Mean accuracy
Older adults	0.73	**Male faces**	0.76
Younger adults	0.79	**Female faces**	0.77

It can be seen from table 4.1 that the younger adults appear to be overall more accurate at the gender discrimination, whilst table 4.1 also indicates no apparent difference in accuracy between male and female faces across groups.

Table 4.2: Mean proportion of correctly identified single gender stimuli across 3 conditions.

Condition	Mean accuracy overall	Mean accuracy older adults	Mean accuracy younger adults
100msec	0.76	0.70	0.79
300msec	0.76	0.72	0.79
Free view	0.79	0.77	0.80

Table 4.2 indicates the quite intuitive finding of higher accuracy overall for the free view condition. However, table 4.2 also appears to indicate that, whilst the accuracy level appears to hold constant across presentation conditions for the younger adults, briefer presentations appear to cause a linear decrement in accuracy for older adults. The same pattern appears to generally hold across both male and female faces as can be seen in table 4.3.

Table 4.3: Mean proportion of correctly identified single gender stimuli for older and younger adults across 3 conditions for both genders of stimuli.

Condition	Group	Stimuli	
		Male faces	Female faces
100msec condition	Younger adults	0.78	0.80
	Older adults	0.72	0.68
300msec condition	Younger adults	0.76	0.82
	Older adults	0.73	0.70
Free view condition	Younger adults	0.80	0.79
	Older adults	0.76	0.79

In order to more closely examine the accuracy levels of both groups in the study, a 2 (Age Group; older adults and younger adults) by 2 (Stimuli; male faces, female faces) by 3 (Condition; 100msec presentation, 300msec presentation, and free view presentation) mixed ANOVA was conducted on the accuracy proportions. This indicated a main effect of Age Group ($F(1,34)=7.69$, $p<.01$), a main effect of Condition ($F(2,68)=5.98$, $p<.01$), and a significant interaction between Age Group and Condition ($F(2,68)=4.04$, $p<.05$). Subsequent analysis of simple main effects indicated significant differences between the accuracy levels of the older adults for the three Conditions ($F(2,68)=8.12$, $p<.001$), but not the younger adults ($F(2,68)=0.12$,$p>.05$). This analysis also indicated that the two age groups differed significantly in accuracy at the 100msec and 300msec conditions ($F(1,102)=11.03$, $p<.01$, $F(1,102)=8.25$, $p<.01$), but not at the free view condition ($F(1,102)=0.82$, $p>.05$). Thus it would appear that the accuracy level of the younger adults remains constant across conditions, whilst the accuracy level of the older

adults is deleteriously affected by the exposure duration change across conditions.

Perceptual bias

The per-subject proportion of trials involving chimeric faces that were responded to with a left bias were calculated for each condition. Grand mean proportions for leftward perceptual biases for younger and older subjects were 0.58 and 0.53 respectively. Grand mean proportions for the 3 presentation conditions across subjects can be seen in table 4.4.

Table 4.4: Grand mean proportions for leftward perceptual biases across subjects for 3 presentation conditions

Condition	Mean proportion
100msec	0.54
300msec	0.57
Free view	0.57

Examination of the data in table 4.4 would appear to indicate a small effect of exposure duration on degree of left perceptual bias between the 100msec condition and the two longer exposure durations across subjects. Means for both groups in the three conditions can be seen in table 4.5.

Table 4.5: Mean left bias proportions for both age groups in three exposure conditions.

Condition	Group	Mean left bias proportion
Older adults	100msec condition	0.51
	300msec condition	0.53
	Free view condition	0.55
Younger adults	100msec condition	0.56
	300msec condition	0.59
	Free view condition	0.58

Examination of table 4.5 indicates that the degree of left perceptual bias elicited from both groups appears to increase as exposure duration increases, with the effect more pronounced for the older adults. The proportion of left perceptual bias for younger adults and older adults at the 100msec, 300msec and free view conditions was subjected to one sample t-tests against 0.5. For younger adults left perceptual biases for all three conditions proved significantly different from chance ($t(21)=3.54$, $p<.01$; $t(21)=4.71$, $p<.001$; $t(21)=3.66$, $p<.01$, respectively). For older adults, left perceptual bias in the 100msec condition was not found to differ from chance ($t(13)=.47$, $p>.05$), whilst left perceptual bias for older adults in the 300msec and free view conditions was found to be significantly different from chance performance ($t(13)=2.52$, $p<.05$; $t(13)=3.87$, $p<.01$, respectively).

In order to more closely examine the degree of left perceptual bias in both groups in the study, a 2 (Age Group; older adults and younger adults) by 3 (Condition; 100msec presentation, 300msec presentation, and free view presentation) mixed ANOVA was conducted on the leftward bias proportions. Results indicated a significant main effect of Age Group ($F(1,34)=4.36$, $p<.05$)

and a significant main effect of Condition ($F(2,68)=4.31$, $p<.05$), the interaction between Age Group and time was not significant ($F(2,68)=0.96$, $p>.05$). Bonferroni corrected pairwise comparisons for the main effect of Condition revealed a significant difference between the 100msec and free view condition only ($p<.05$).

Therefore the most parsimonious interpretation would indicate that the older adults demonstrate a reduced bias overall compared to the younger adults overall. However, the important difference being that at the shortest exposure duration the older adults display no bias whilst the left bias is already significantly above chance for the younger adults. The degree of left bias for both groups increases with exposure duration. Although the interaction between group and condition was found to be non-significant, there is also a trend in the means insofar that the younger group is already approaching ceiling at 300msec of exposure whilst the older adults' bias continues to increase between 300msec and free view.

Reaction times

The study also examined potential differences in reaction times to single gender faces and chimerics faces, in both groups, across the three presentation conditions. As there is no correct answer, per se, for the task when chimeric faces are displayed, and as my primary interest was in differences between the two types of stimuli across groups and conditions, all responses to single gender stimuli were pooled, disregarding accuracy. Mean reaction times for older adults and younger adults were 997 msec and 870 msec respectively. Mean reaction times for single gender faces and chimeric faces were 852 msec and 986 msec respectively. Mean reaction times for the

two groups for both types of stimuli can be seen in table 4.6, which indicates that latencies to chimeric stimuli appear to be higher for both groups.

Table 4.6: Mean reaction times in milliseconds for older and younger adults for single gender and chimeric faces.

Group	Stimuli type	
	Single gender	Chimeric
Older adults	930	1063
Younger adults	802	937

A description of the mean reaction times for the two groups for the three presentation conditions can be seen in table 4.7, which illustrates that, although there is some evidence for longer latencies in the older adults group across all conditions, compared to the younger adults, it is particularly pronounced for the free view condition.

Table 4.7: Mean reaction times in milliseconds for older and younger adults for 100msec, 300msec and free view conditions.

	Condition		
Group	**100msec**	**300msec**	**Free view**
Older adults	774	787	1429
Younger adults	719	751	1140

A description of the mean reaction times for the two groups for the three presentation conditions for both stimuli types can be seen in table 4.8. This will form the basis of the statistical analysis below.

Table 4.8: Mean reaction times in milliseconds for older and younger adults for 100msec, 300msec and free view conditions for single gender and chimeric faces.

		Condition		
		100msec	**300msec**	**Free view**
Older adults	**Single gender**	761	755	1275
	chimeric	787	819	1584
Younger adults	**Single gender**	700	719	988
	chimeric	738	782	1292

In order to examine the differences in reaction times in detail, per-subject reaction times were entered into a 2 (between Group; older and younger adults) by 2 (within Face Type; single gender and chimeric faces) by 3 (Condition; 100msec, 300msec and free view) mixed ANOVA. Significant main effects were found for Face Type ($F_{(1,34)}$=20.78, p<.001), and Condition ($F_{(2,68)}$=16.10, p<.001), however, a significant interaction between these two factors was also revealed ($F_{(2,68)}$=12.56, p<.001). No other main effects or interactions were found to be significant. Analysis of the simple main effects indicated significant effects of Condition on latencies for both chimeric faces ($F_{(2,136)}$=22.40, p<.001) and single gender faces ($F_{(2,136)}$=7.78, p<.001), however it also indicated a significant difference in latency for the free view condition only ($F_{(1,102)}$=47.79, p<.001) with no difference in latencies to chimeric or single gender stimuli at either the 100msec or 300msec presentation conditions.

Summary

Accuracy

Analysis of the accuracy of the participants to make gender decisions to faces presented at differing exposure thresholds revealed age related differences in performance. Firstly, the younger adults were more accurate overall, but in addition, a significant interaction revealed that the degree of accuracy for the younger subjects held constant for the three exposure durations, whilst accuracy levels for the older adults was adversely affected by limiting stimuli exposure: only the free view condition generated equivalent degrees of perceptual accuracy in the gender decisions between the two age groups and lower exposure times generated a linear decrement in accuracy for the older adults.

Perceptual bias

The calculation of the proportion of chimeric face trials that were preferentially responded to on the basis of the information available on the left side of the face was calculated for each subject in the two age groups. Overall these results indicated that the degree of leftward bias was lower at the 100msec duration than at the two longer exposure durations. Further analysis indicated that with the exception of the older adults at 100msec exposure, all other conditions generated a significant leftward bias in the two groups. No interaction was obtained, which in the light of the results of the t-test calculations compared to chance performance, is interpreted to demonstrate that the older adults demonstrate a reduced perceptual bias overall. The older adults demonstrate no significant bias at the shortest exposure duration, whilst the younger adults do demonstrate a significant leftward perceptual bias at this level, with both groups demonstrating an

increased perceptual bias in the free view condition relative to the 100msec condition. Although no significant interaction was obtained, overall means would also appear to indicate that the younger group has already approached a ceiling level at the 300msec exposure condition whilst the degree of bias for the older adults continues to increase from the 300msec to the free view condition.

Reaction times

Overall means appeared to indicate that older adults had higher latencies, and that latencies to respond to chimeric images were higher than latencies to single gender faces. However, ANOVA results indicated that there were no effects of age on latency to responses to either chimeric or single gender images within the three conditions, however, an interaction in the ANOVA revealed an increase in latency for responses to chimeric relative to single gender images in the free view condition.

Discussion

Accuracy and latency

Only the older adults demonstrated deterioration in accuracy at shorter exposure durations whilst accuracy for the younger group held constant, so only within the free view condition did I obtain equivalent degrees of accuracy to identify single gender stimuli. Unlike the chimeric face studies of Levine and Levy (1986), Moreno et al (1990), Cherry et al (1995) and Failla et al (2003), who all employed a free view paradigm, the present study also collected latency measures and observed that latencies between older and younger adults did not differ significantly. Response time differences between younger

and older adults are common in the literature and in light of this is a surprising result.

Gunning-Dixon et al (2003), for example, reported how their older sample were slower than their younger sample of adults to make emotion and age identification judgements to faces and the literature commonly reports the phenomenon of older adults being slower in this type of task. Indeed, Tisserand and Jolles (2003) suggest that a potentially overarching factor in cognitive aging that may ultimately be related to subsidiary processes such as declines in memory may in fact be processing speed. Indeed Lindenberger and Baltes (1997) reported a stronger relationship between age and processing speed than between age and reasoning or memory.

Obler, Woodward and Albert (1984) present evidence that older adults may even be differentially slow at processing face stimuli relative to verbal material. Obler et al exposed younger and older subjects to same-different tasks for verbal and facial material (involving top and bottom halves of photographs of faces) presented to either the left or right visual fields. They reported that it took their older subjects significantly longer to achieve an accuracy criterion of 80% for the face stimuli compared to the verbal stimuli. Although they concede that they could not be certain that both tasks were equated for difficulty they argue that this finding indicates that as subjects age, judgements involving facial stimuli become more difficult than their other task involving syllables. However they reported that no effects of age for raw error, reaction time scores, or laterality of stimuli were found. They also suggest that their one significant effect could be due to either more practice in reading or the higher visual complexity of the face stimuli.

It would appear that the present results can best be explained when considering the latency and accuracy data together. It seems that in the present study that the older adults sacrificed accuracy for speed.

Perceptual bias and eye movements

I hypothesised that increasing exposure duration would lead to an increase in the degree of leftward perceptual bias obtained to chimeric stimuli. This hypothesis was supported by the present results. In each exposure duration, with the exception of the 100msec condition for older adults I obtained a leftward perceptual bias that was significantly higher than chance, and, in addition, results indicated that the degree of bias in the free view condition was significantly higher than that obtained in the 100msec condition. This result is in line with the finding of David (1993) who obtained a significant perceptual bias to emotion based chimeric stimuli with an exposure duration of 120msec, but in the present case the results have been obtained with gender based stimuli, which invoke perceptual decisions I have suggested may lie closer to basic face processing mechanisms. This result considerably strengthens the claim made in experiment 3 that eye movements enhance perceptual biases to chimeric faces, as in this case the data was obtained under directly comparable conditions. Thus, although the present findings are in line with the results of Ferber and Murray (2005) in demonstrating that perceptual biases can be obtained in the absence of eye movements, they supplement them with the strong conclusion that eye movements do indeed enhance perceptual biases, in line with the prediction of Vaid & Singh (1989), Sakhuja et al (1996) and Heath et al (2005).

Perceptual bias and older adults

With regard to the relationship between aging and perceptual bias I have interpreted the results to indicate reduced perceptual biases overall in the older adults compared to the younger adults. Additionally, I observed that a significant bias was obtained from the younger group at all exposure durations, whilst the perceptual bias obtained from the older adults at the shortest exposure duration was not significantly different from chance. Furthermore, I observed that both age groups demonstrated significantly greater leftward biases at the free view condition compared to the shortest 100msec condition (which should preclude eye movements). Also group means indicate that the younger group has already approached a ceiling level in terms of perceptual bias, at the 300msec exposure condition, whilst the degree of leftward perceptual bias for the older adults continues to increase from the 300msec to the free view condition. Therefore I can conclude that both groups demonstrate an increase in the degree of perceptual bias produced with increasing exposure to the stimuli, and that the younger group demonstrate significantly higher biases overall. In combination with the finding that the older adults do not demonstrate a significant bias at the shortest exposure condition this can lead us to conclude that perceptual biases to these stimuli were strongly influenced by the age of the participants.

T-test analysis examining the degree of left perceptual bias compared to that which would be obtained through chance alone shows that precluding eye movements by reducing exposure duration has a more deleterious influence on the perceptual biases of older adults. Clearly a caveat to this conclusion, which potentially confounds firm conclusions, is the finding that the older adults are less accurate in the 100msec and 300msec conditions in their identification of single gender faces in the task, and thus that lower accuracy

and lowered biases are related through mechanisms of higher degrees of guessing at the shorter exposure time conditions. However, in the free view condition, the results indicate that both groups are equally accurate. Additionally, I have reported no influence of age on reaction times, thus a reliable comparison of perceptual biases can be made in the free view condition. Here I observed lower perceptual biases in the older adults in comparison to the younger adults. Thus in the case of the free view condition it would appear that the diminished tendency to select the gender based on the left hand side of the face in the elderly sample fits well with theories of selective right hemisphere aging and the HAROLD hypothesis.

Regarding a mechanism to explain this finding, I previously postulated that the tendency to first inspect the left side of the face in the younger sample of experiment 1 reflected the fact that when the face is first presented, fixation is in the centre of the face. The left hand side of the face, I suggested, projects to the right hemisphere activating the neural structures there that are believed to preferentially respond to face stimuli (or any complex configurational pattern; Rhodes, 1993, Burt and Perret, 1997). I argued that the same does not occur for the right hand side of the face, therefore making the left hand side of the face initially more salient, with this increase in salience driving the tendency to make a first saccade to the left visual field. Both aging hypotheses can accommodate diminished right hemisphere activational biases in the present task, and therefore also predict, by this argument, a diminished tendency to find the left side of the face more salient. This theory is further strengthened (albeit with a cautious eye on accuracy levels to single gender stimuli in this condition), by the finding that older adults demonstrated no significant degree of perceptual bias in the 100msec condition, where they were precluded from generating saccades to the stimuli.

Additionally, it would appear that the arguments of Ferber and Murray (2005) are less, if at all, applicable to older adults, whilst the arguments of Vaid & Singh (1989), Sakhuja et al (1996) and Heath et al (2005) of an influence of scanning habits on perceptual biases would appear to apply to both groups. Indeed one may speculate that scanning habits are the only influence on perceptual biases on older adults, whilst younger adults additionally demonstrate a perceptual bias which is also driven by an inherent right hemisphere dominance in the task itself, thus leading to an enhanced degree of bias in the younger adults.

Although I have reviewed evidence supporting or disputing the relative merits of views of age related changes in the brain such as the Differential Aging or HAROLD hypotheses, it is as yet unclear precisely why older adults would display both differential responses and differential patterns of functional activation in perceptual or memory tasks relative to younger adults. Strong explanatory theories for the differential behaviour of older and younger adults have been postulated in terms of compensatory behaviour and de-differentiation. Compensatory brain activation, particularly when leading to more bilateral brain activity is particularly complementary to the HAROLD model of the effect of the aging process on the brain.

Compensatory changes in the older brain

Reuter-Lorenz et al (2000) report evidence for compensatory frontal bilateral activity in older adults in a memory task, whilst Gutchess et al (2005) also imply a compensatory role for frontal activity in their older sample. With regard to face processing, Grady (2002) observed evidence for patterns of differential brain activity when comparing responses to degraded and non degraded face matching in younger and older adults through fMRI which

involved differentially increased prefrontal activity in the older sample. Grady took this as symptomatic of earlier cognitive effort in the older group and that whilst prefrontal activity may be employed in a task specific way in younger groups, prefrontal activity is related to tasks that are more demanding in the older sample independent of the specificity of the task itself. Thus the case may be that differing patterns of responses observed in this experiment are symptomatic of differential cognitive experience of effort in a given task.

Indeed Grady, McIntosh, Horwitz and Rapoport (2000) provide evidence for functional compensation in face processing in other areas of the brain. Grady et al report evidence of a strong degree of functional plasticity in the older adults in their study of face matching. Employing PET scanning they exposed younger and older adults to a face matching task involving visual noise and degraded and non degraded face stimuli. Scan data revealed that whilst most of the areas that were more active in the younger group in both the control condition and the non degraded condition were in the right hemisphere, they were in the left hemisphere for the older group. Furthermore, regions correlated with performance in the task differed between the two groups, with the younger group showing a relationship between the fusiform gyrus and their performance, and the older group showing a relationship between performance and activity in the occipital lobes, posterior cingulate and subcortical structures. Results were in fact indicative of increasingly bilateral involvement in face matching in the older adult group, possibly related to a compensatory mechanism indicative of differential face processing (or indeed visual processing) in the older group.

An earlier benefit of using cross-hemispheric processing in the elderly: Reduced perceptual bias?

Reuter-Lorenz, Stanczak and Miller (1999) reported that a processing boost from recruiting both hemispheres is called on earlier in older than younger adults. They exposed younger and older adults to a letter matching task, with lateralised target and search stimuli, thus requiring either a within or across hemisphere comparison. Results indicated that whilst younger adults had no difficulty with any positional manipulation of stimuli, the older adults showed an across hemisphere advantage at the medium and difficult levels of task complexity, which was only demonstrated by the younger adults at difficult level of complexity. Thus older adults demonstrated an advantage for across hemisphere trials at a lower level of complexity than the younger adults. The authors suggest that older adults gain an advantage for bi-hemispheric processing at levels of task complexity that can be dealt with by employing unilateral processing in the younger group. Such bi-hemispheric recruitment may assist the brain in meeting higher processing demands in a compensatory manner to combat neural decline related to ageing.

Thus with regard to the present findings, if older adults place more reliance on cross hemispheric involvement with lighter loads of task complexity, due to experiencing the task as more effortful, it could therefore be predicted that this would result in lowered perceptual biases in older groups with chimeric faces tasks as was the case in the present study.

Functional de-differentiation in older adults

Additionally, an explanation for differential face processing in older adults relative to younger adults can be viewed in terms of functional de-differentiation in the older adult brain. The theory takes a view of differential

cortical recruitment in the elderly, which postulates that areas that become specialised for a given task in younger adults become more generalised as we age. Park et al (2004) argue that age related slowing in perceptual tasks is a modulator of age related variance on many activities involving cognitive processes, and thus that age related slowing in perceptual comparison tasks is related to functional de-differentiation in high level sensory cortex. They conclude that age related de-differentiation might be found in numerous brain structures beyond the frontal cortices.

Park et al (2004) examined the phenomenon of increased bilateralism in older adults in what are typically unilateral frontal tasks in younger subjects. Arguing that the functions of the frontal lobes are not yet fully understood, they argue that evidence to date does not necessarily imply an explanation in terms of age related de-differentiation, and does not address whether the issue relates to recruiting more neural areas that are specialised for a task, used generally, or indeed are purely evidence of a dysfunctional recruitment related to the aging process. Park et al argued that areas of ventral visual cortex are in many ways better understood than the frontal cortex, with identified areas that are differentiated and respond maximally to places, faces and words, and thus that such areas are better equipped to be examined in an imaging study to explore supposed de-differentiation in older adults. Park et al exposed older and younger adults to pictorial stimuli of faces, pseudo-words, houses, chairs and scrambled control images in an fMRI scanner. They reported strong evidence of neural de-differentiation in older adults in ventral visual cortex. Results, based on examining activity in regions of ventral visual cortex were in fact strongly in line with a de-differentiation hypothesis.

Payer et al (2006) further explored this view, and reported that older adults decline in specificity of areas of visual ventral cortex also occurs when

working memory is engaged, and argue that the ventral visual system is subject to age related change in function, and thus that such changes are not restricted to higher areas in frontal cortex. Park et al used face and place (house) stimuli to explore age related differences in neural specialization with fMRI in a working memory task. They identified each participant's most active voxels to the two types of stimuli after they were exposed to sets of one category for encoding, followed by a present-not present decision to a probe. Results indicated that the older adults had decreased neural specialisation in ventral visual cortex and simultaneous increased activity in prefrontal cortex when compared to the younger group.

Results from Payer et al were examined firstly by defining voxel based face and house areas in the two groups in ventral visual cortex. This revealed that younger adults had significantly fewer shared voxels than the older group. They then turned to examine how active these regions were in the two groups during encoding the two types of stimuli. Analysis indicated that the younger group showed more differentiation than the older group in house voxels response to house stimuli than the older group, and a similar finding was found for the young group for face voxels to face stimuli, although statistically less robustly. Turning to analysis of the whole brain, their findings revealed that prefrontal cortex regions were more diffusely activated in the older group. During the encoding phase results indicated predominantly right prefrontal cortex activation in the younger group and bilateral activation in the older group. Similar findings were found when the analysis focussed on prefrontal response to the probe, although again results were statistically less robust.

Payer et al suggest that their findings of increased activity in prefrontal cortex in the elderly at the same time as a decrease in differentiation would

suggest that the prefrontal cortex is engaged in a compensatory mechanism relative to decreased ventral visual cortex functional specialisation in the older adult. Thus highlighting the importance of respecting the interconnectivity of the brain when examining age related change. In light of this, the present findings of a reduction in the degree of left perceptual bias could possibly be additionally accommodated within a model of functional de-differentiation related to the aging process.

Conclusion

The present study provides evidence for a temporal component to perceptual biases, namely that an increase in exposure duration to chimeric stimuli results in an increase in the degree of leftward perceptual biases demonstrated in right handed participants, irrespective of age. Analysis of group differences revealed fundamental differences in the perceptual activity of younger and older subjects, namely that younger subjects demonstrate significant perceptual biases to chimeric face stimuli even at sub-saccadic exposure durations, whilst older adults only demonstrate leftward biases that are significantly higher than chance level in conditions where sufficient time is allowed for the participants to generate eye movements. I therefore argue that the findings of Ferber and Murray (2005) appear to be more applicable to younger adults whilst it would appear that all adults gain an enhanced perceptual bias when permitted to make eye movements. Differential perceptual activity as displayed in the older adults in the present study can be viewed in terms of either reduced right hemispheric function, or increased bilateral function as a consequence of experience of a task as more effortful, related to the aging process. Additionally the present findings can be interpreted in terms of a view of the older adult brain experiencing functional

de-differentiation of areas of ventral visual cortex that are specialised for face perception in younger adults which become less specialised as a result of the aging process.

Chapter 3

Introduction

Chapters one and two have explored, both through review and through experimentation, right hemisphere dominance in certain types of tasks involving decisions to visual stimuli. Experiment 1 indicated, for example, that visual attention, measured through its correlate in eye movements, is preferentially initially deployed to the left side of the image when participants take part in a gender decision task to facial stimuli. It was proposed that the right hemisphere has demonstrable influence on how an individual approaches this type of task.

However, it is known that damage to the right hemisphere, resulting in the syndrome of hemispatial neglect, results in such patients preferentially choosing to base their decisions on the right side of chimeric faces (Mattingley, Bradshaw, Phillips & Bradshaw, 1993), whilst studies such as that conducted by Walker, Findlay, Young & Lincoln (1996) indicate that such patients have a rightward bias in the numbers of fixations they make to such stimuli. The next section of this thesis will focus on another aspect of how one's visual attention can be influenced, not just by the characteristics of what is looked at, but also by the characteristics of the goal of the individual. Chapter 3 will again employ analysis of participants eye movement behaviour in order to examine how both stimulus and goal driven properties of a task are combined to influence where one will allocate one's attention (or have it allocated). Additionally, chapter 3 will also examine how such different aspects of visual attention can fractionate when an individual suffers damage to the right hemisphere.

Historically characterised as passive or active, the allocation of visual attention can be both stimulus-driven and goal-driven, or alternatively bottom-up or top-down controlled. By either definition, attention can be said to be deployed deliberately by the observer with regard to their objective, or directed to a stimulus almost entirely by some aspect of the image (Egeth & Yantis, 1997).

Stimulus and goal driven visual attention

A number of studies have shown that attention can be captured in a *stimulus-driven* manner by new items that appear in the visual scene with an abrupt onset (e.g., Theeuwes, 1994), and that capture also affects overt attention: in a search task subjects frequently make erroneous saccades to an abrupt onset distracter before fixating the target, a behaviour that is likely to explain the increased detection time observed in a range of studies (Irwin, Colcombe, Kramer & Hahn, 2000; Theeuwes, Kramer, Hahn & Irwin, 1998; Theeuwes, Kramer, Hahn, Irwin & Zelinsky, 1999).

Theeuwes et al (1999), for example, examined the eye movements of subjects in a study in which "goal-directed selection was pitted against stimulus-driven selection". Subjects were directed to make a saccade to a colour singleton target amongst distracters. In the abrupt onset distracter condition an additional distracter would appear in the display. Theeuwes et al reported that manual latencies to identify the target were slowed by the abrupt onset. Additionally, with regard to eye movement behaviour, it was reported that the eyes often went in the direction of the abrupt onset distracter rather than the target, a behaviour that was even observed to occur when the abrupt onset was on the opposite side of the display from the target. The capture effect of the abrupt onset was particularly strong when the onset appeared at

the same time as the target. Theeuwes et al observed that fixation durations for saccades to the abrupt onset distracter were very short, suggesting that two eye movements were programmed in parallel, with a saccade to the target initiated quickly after a reflexive saccade toward the distracter. If the abrupt onset appears too long after the target then programming of the goal directed saccade will be complete and a saccade to the distracter will not occur.

On the other hand, Folk, Remington and colleagues (Folk, Remington & Johnston, 1992; Folk, Remington & Wright, 1994) have shown the importance of *goal-driven* attentional control settings in mediating capture. Using cueing paradigms they showed that validity effects were obtained only when the cue and the target shared a relevant feature, for example, responses to a colour target were slowed down when preceded by an invalid colour cue, but not by an invalid abrupt onset cue. Their contingent capture hypothesis states that capture is never purely stimulus driven but depends on the visual features the attentional system has been set up to respond to. Theeuwes et al (1999) however argued that their finding of goal directed saccade disruption by abrupt onset distracters was incompatible with this view, as if it were the case then their participants should have been able to simply disregard a distracter with an abrupt onset if their attentional set was goal directed to a colour singleton.

To elucidate the contribution of *both goal and stimulus driven* factors in oculomotor capture in a single visual search paradigm, Ludwig and Gilchrist (2002; 2003a) asked subjects to search for a coloured target among three distracters and signal its location with a saccade. An additional irrelevant distracter was presented to the left or right, appearing with or without an abrupt onset, and its colour was either similar or dissimilar to the target. They found that similar distracters indeed disrupted saccade programming

more than dissimilar ones. However, capture was particularly pronounced when the similar distracter had an abrupt onset. These results demonstrate that stimulus-driven oculomotor capture by abrupt onset distracters can be modulated by distracter-target similarity.

Distinct neural pathways for reflexive and goal driven saccades?

As Ludwig & Gilchrist (2003a) point out, such a modulation of oculomotor capture by target similarity has implications for theories and models of saccadic programming. One idea that is prevalent in the literature of oculomotor behaviour is that of distinct neural pathways for different types of saccades. Neuropsychological evidence has so far supported the idea that stimulus-driven and goal-driven control are dissociable in terms of their underlying neural pathways (Gaymard, Ploner, Rivaud, Vermersch & Pierrot-Deseilligny, 1998; Guitton, Butchel & Douglas, 1985). Two types of eye movements can be described; stimulus driven or 'reflexive' saccades triggered by a sudden luminance onset in the visual field, and more goal driven or 'voluntary' saccades. The stimulus driven saccades are thought to be mediated by a fast route from striate cortex and the parietal eye fields in the intra parietal sulcus, into the superior colliculus (the parieto-tectal route, and additionally a direct retino-tectal route is available), whilst the goal driven eye movements are assumed to depend on the frontal eye fields and corresponding projections to the superior colliculus and the brainstem saccade generator. The efferent tract from the parietal region projects through the posterior internal capsule, whilst the efferent tract from the frontal eye field conversely travels through the anterior part of the internal capsule (Condy, Rivaud-Péchoux, Ostendorf, Ploner and Gaymard, 2004). On the basis of their own findings of rapid corrective saccades, Theeuwes and his colleagues (1998,

1999) have explained oculomotor capture in terms of a race between a stimulus-driven saccade program associated with the abrupt onset distracter and a goal-driven program for the correct target-directed saccade.

However, Ludwig and Gilchrist (2002, 2003a) have argued that the goal-driven modulation of capture by target similarity is not consistent with a strict dichotomy of stimulus driven saccades mediated by a parieto-tectal route, and goal driven saccades dependent on the frontal eye fields. They argue that the predominantly magnocellular projections from V1/ parietal eye fields into the superior colliculus are not likely to convey colour identity, thus they indicate that it is hard to see why onsets in the target colour are so much more disruptive than onsets of a similar luminance in any other colour (given that the magnitude of the luminance transients was equated in their study). Instead, they suggest, it appears that bottom-up signals (from abrupt onsets) are combined with top-down signals concerning target similarity information to jointly determine an item's salience.

Indeed the idea that stimulus-driven and goal-driven signals converge onto a common oculomotor salience map is central to a recent computational model of saccade programming (Trappenberg, Dorris, Munoz & Klein, 2001). Trappenberg et al stress that a model of oculomotor behaviour should be able to encompass both top down and bottom up influences. They centre their model on the intermediate layers of the colliculus, which receives input from a broad range of cortical and sub-cortical structures involved in the generation of saccades. By artificially modelling firing rates of collicular fixation, build-up and burst neurones (see Munoz & Everling, 2004) in theoretical nodes, both exogenous (marginally processed sensory input) and endogenous (voluntary inputs related to instructions and subject expectancy) visual signal inputs are modelled to converge in a theoretical construct of the intermediate colliculus.

Within Trappenberg et al's modelled colliculus, lateral interactions involving both excitations and inhibition occur. The model takes the view that the variability of saccadic reaction times in various paradigms is influenced by a mechanism of dynamic integration by competition. Differing experimental conditions are modelled by means of manipulations of signal amplitude and signal input time, which reflects exogenous and endogenous signals either travelling directly or delayed by the requirements of higher processing with endogenous signals. The model can be shown to account for saccadic behaviour in paradigms such as fixation-stimuli onset temporal gaps, neuronal buildup activity, the effect of distracters, antisaccades, express saccades, and target location probability.

In fact, more recently, Godjin and Theeuwes (2002) have argued for a more integrated model of saccadic programming on the basis of their own research. Their more recent findings in fact favour a competitive integration model rather than a winner-take-all horse race between goal and stimulus driven saccade programming, and proposes, in line with the model of Trappenberg et al (2001), that exogenous and endogenous saccadic control signals converge on a common saccade map were both types of information can be combined.

Related to this, Walker and McSorley (2006) have examined saccadic latencies to single voluntary, single reflexive, two-step voluntary followed by reflexive saccades, or two-step reflexive followed by voluntary saccades. Their results indicated good evidence for the programming of parallel saccades, in that latencies for second saccades were lower compared to the equivalent single saccade condition. Additionally, evidence of competitive interactions in the programming was deduced from the findings of latency differences for the first saccade when the second was in the opposite direction compared to when

both saccades were in the same direction, thus the authors concluded that this could be taken as evidence that both saccades were generated on a common motor map.

Visual search and brain injury

A number of studies have employed the anti-saccade task (Hallet, 1978) to investigate the relationship between voluntary (goal-driven) and involuntary (stimulus-driven) orienting responses. In this task participants are required to make a saccade away from a target that suddenly appears in the peripheral visual field. Successful performance in this task requires participants to inhibit the stimulus driven orienting response to the target, and instead to generate a voluntary orienting response in the opposite direction to the stimulus.

Difficulties with the inhibition of eye movements have been demonstrated in patients with frontal lobe damage, with such patients displaying increased error rates in the anti-saccade task (Guitton et al, 1985). The ability to simply look towards a visual target is unimpaired in such patients. As such, a prevalent assumption is that posterior brain regions (perhaps in the form of a parieto-tectal route) are sufficient for the generation of stimulus-driven saccades. Goal-driven selection however is deemed to depend on the frontal lobes, or some substructure within the frontal lobes (Everling & Fischer, 1998; Munoz & Everling, 2004).

Within the neuropsychological literature, goal driven search and selection deficits are often reported in patients demonstrating the syndrome of hemispatial neglect following stroke. Neglect, a lack of contralesional spatial awareness following brain injury (Karnath et al, 2001) is particularly prevalent following injury to the right side of the brain, in the inferior parietal lobule,

although it can involve damage to dorsolateral premotor and medial frontal regions or subcortical structures (Vallar, 1998), although debate with regard to specific anatomical correlates of the syndrome continue (Karnath et al, 2001; Milner and McIntosh, 2005). With regard to eye movements, patients with hemispatial neglect fail to make leftward saccades when searching for a target or are slower and make smaller amplitude saccades to left space if they do perform them (Walker and Findlay, 1996). They further have characteristic difficulties in visual search tasks, where subjects need to find a target in an array of distracter stimuli. Typically such tasks are defined as either simple search tasks, where the target 'pops out' due to a unique defining feature, or require more attentional resources due to the target differing from the distracters by a conjunction of features. Such tasks can thus also be described as involving low attention parallel search or higher attentional focus serial search, with only the latter type of search having a relationship between search time and the number of distracters.

Visual search tasks have proven to be a useful tool in identifying attentional deficits in the syndrome of hemispatial neglect. Indeed Harvey, Olk, Muir, and Gilchrist (2002) studied two patients, one of which had recovered from neglect and another who had a chronic manifestation of the condition whilst they participated in a visual search task. Results indicated that lateralised search failures in the patients performance allowed for differentiation of the two patients. Indeed many researchers have examined the performance of patients with hemispatial neglect in tasks that require visual search and consistently report failures or difficulties in the patients undertaking the task.

Robertson and Eglin (1993) summarise different aspects of deficits in attentional search in patients with hemispatial neglect with patients displaying

a bias to begin scanning at the most ipsilesional item in a given search array, a drop in the speed of their search rate, and a problem with disengaging attention from the ipsilesional field to search into the neglected field. Rapcsak, Verfaellie, Fleet and Heilman (1989) studied patients with hemispatial neglect in a geometric shapes cancellation task. They reported that left sided neglect became more pronounced in more difficult search conditions were higher degrees of selective attention were required.

Whilst monitoring eye movements, Behrmann, Watt, Black and Barton (1997) studied similar patients. They reported that such patients, relative to controls, found significantly fewer targets, had a significantly lower number of fixations and spent less time on the left side of the display compared to the right. Finally, they spent more time and made more fixations on the right side of the display where they tended to begin their search, becoming increasingly less likely to make fixations the further left across the board they travelled.

Karnath and colleagues (Karnath, Niemeier and Dichgans, 1998; Karnath and Niemeier, 2002) employed an ingenious 'lightbulb shaped room' to study the eye movements of patients engaged in visual search tasks in an array that surrounded the participant. Patients were reported to search a smaller part of the array, with gaze deviated ipsilesionally. Altering task instructions to focus attention only on a rightward area of the whole array actually resulted in the left side of this subsection being ignored by the patients who had previously searched it when instructed to search the entire array.

A further issue relating to visual search in patients with hemispatial neglect pertains to whether their difficulties lie in the more attentionally demanding type of search tasks, involving conjunctive search or whether they have difficulty in simple feature search tasks which healthy participants

appear to do with enormous ease. Marsel Mesulam (1999) reviews evidence indicating that such patients have more problems in search tasks where the target is identifiable through a more intensive serial search rather than a target that pops out of the display. This debate in the literature is also examined in a recent paper by Behrmann, Ebert and Black (2004).

Aglioti, Smania, Barbieri and Corbetta (1997), for example, studied visual search performance in brain damaged patients, both with and without neglect symptoms. Visual search was assessed with two cancellation tests, set up to make the search easy in the pre-attentive condition and effortful in the attentive condition, were the target had a lower salience and was presumed to require focussed attention. Results indicated that the neglect group made more omissions on the attentive compared to the pre-attentive search condition compared to other groups studied, and, when scanning to the left, made lower amplitude explorations in the attentive compared to the pre-attentive condition. Aglioti et al conclude that the impairment demonstrated in the more difficult search task suggests that pre-attentive processing is comparatively spared in these patients.

Eglin, Robertson and Knight (1989), in line with this, reported that patients demonstrated performance speeds that were comparable to those seen in a slower serial search approach in both types of search tasks. Eglin et al also reported that search for targets in the neglected field was slowed due to distracters in the intact field more profoundly in the conjunctive search task.

Pavlovskaya, Ring, Groswasser and Hochstein (2002) used patients with right hemisphere damage and neglect in both easy pop out visual search and more attentive conjunction search. Results indicated that feature based search is vulnerable to neglect, as patients had more difficulty locating targets in the left when the array was presented centrally whilst when the array was

located laterally there was a large difference in performance depending on whether the array was in the neglected field or intact field.

In another case study, Laeng, Brennen and Espeseth (2002) examined the performance of a patient with hemispatial neglect and a right hemisphere lesion in visual search, again when search was simple and parallel, or in another more difficult serial search condition. Interestingly, the patient demonstrated a performance profile whereby latencies for false negatives and correct positive trials were both faster than correct positive latencies in the simple search (where targets are expected to pop out), whilst in the more difficult parallel condition latencies for correct and incorrect negative trials were both slower than correct positive identifications of the target trials. The authors argue that the patient could use pre-attentive information to support parallel search, but errors occurred in the search, resulting in an incomplete pre-attentive search in the parallel search condition.

In a recent examination of the debate on proposed intact feature based, or 'pre-attentive' search in patients with neglect, Behrmann, Ebert and Black (2004) argue that all types of search, whether supposedly pre-attentive or not, require some degree of attentional processing on the part of the participant and thus attention is more appropriately viewed with regard to competition between stimuli representations.

Indeed, visual search dysfunction has also been demonstrated in patients without evidence of hemispatial neglect. Mapstone et al (2003) monitored participants eye movements in a visual search task in order to examine differences in performance between controls and patients with unilateral left and right hemisphere lesions without neglect. Their results indicated that both patient groups detected significantly fewer targets in their contralesional hemispace, however, results also indicated that the right

hemisphere group made significantly fewer fixations into the contralesional hemispace compared to the ipsilesional hemispace. The size of this asymmetry was significantly larger in the right hemisphere group than in the left hemisphere group or control group, with the former group demonstrating a profile of fixations that was shifted to the right, unlike the left hemisphere group who matched controls.

Fimm et al (2001) examined groups of patients with left or right sided exclusively subcortical lesions such as basal ganglia, internal capsule and thalamus, without evidence of clinical visual neglect in a visual scanning task. Participants were instructed to locate a target by employing a top left to bottom right strategy, as would be seen in reading. Fimm et al reported that 7 out of 8 of the right hemisphere patients demonstrated impairments in the processing of information in the contralesional side, whilst only 2 patients with left hemisphere lesions demonstrated contralesional impairments. Thus the authors speculated that basal ganglia regions, such as putamen and posterior limb of internal capsule are a crucial aspect of the orienting of visual attention, playing an important part of the anterior and posterior attentional network.

Brain injury and inhibition of irrelevant stimuli

Therefore, either with regard to simple feature based 'pop out' search or more attention demanding conjunctive search, clear deficits have been demonstrated in patients with right hemispheric lesions, both in the presence and absence of hemispatial neglect. However, it is of interest to examine the relative contributions of both top-down and bottom-up features in search in patients with right hemisphere lesions. In other words, whilst it is clear that such patients may demonstrate dysfunction in search, it is less clear how well

such patients may be able to suppress irrelevant distracters in what would in other terms be a simple feature based search for a colour singleton. To this end, the following study will examine the performance of healthy older adult controls and patients with both cortical and sub-cortical lesions in an adaptation of the Ludwig and Gilchrist (2002) paradigm.

Firstly, findings are reported where stimulus-driven and goal-driven capture is investigated using the paradigm developed by Ludwig and Gilchrist (2002; 2003a) in a patient with a temporo-parietal lesion. This patient is particularly interesting because the frontal cortex is spared.

Experiment 5: A report of oculomotor control impairments in a right temporo-parietal lesioned patient in an oculomotor capture task.

Method

Healthy participants

Twelve elderly control subjects age matched to the patient TH (4 male, 8 female; mean age 73.4, SD 4.7) took part in the experiment and were reimbursed for travel expenses.

Patient

At the time of testing TH was a 73 year old male with 9 years of full time education. A CT scan revealed a small discrete right temporo-parietal infarct with no damage to white matter tracts and no evidence of frontal impairment

(see Figure 6.1). He showed no hemiparesis, nor hemianopia on perimetry testing.

His performance on the Behavioural Inattention Test (BIT, Wilson, Cockburn & Halligan, 1987) was 129/146, which was at the cut-off mark below which a diagnosis of hemispatial neglect would be given. However, on tasks such as star cancellation he scored 50/54 with omissions found evenly over the page suggesting that neglect was not present.

Extinction testing was formally assessed on a laptop with a 36cm screen with stimuli at a viewing distance of 60cm. Stimuli (asterisks of 0.24° high) were presented for 100 msec, either unilaterally to the left or right of the screen, or simultaneously on both sides, at either 2.2° or 4.4° from the centre of the screen. Seventy trials (including 10 catch trials) were presented, 10 for each condition and eccentricity. The patient performed perfectly on all trials.

He was also assessed with the WAIS III–R (Wechsler, 1981) on which his general performance was above average. In the verbal performance subtests he scored below average on Vocabulary (9) but above average on Information and Digit Span (12 and 11 respectively). Again his scores on the performance subtests were all above average, scoring 11 on all tasks (Picture completion, Block design, and Object assembly). Similarly his premorbid IQ could be judged above average as his performance on the National Adult Reading Test (Nelson & O'Connell, 1978) indicated an estimated IQ of 111.

Apparatus and stimuli

Example displays are shown in Figure 5.1. Placeholder displays consisted of a central, grey circular disk (with a radius of 0.3°) that served as the fixation point and four placeholders indicating the possible target locations. In addition there was a fifth placeholder to the left or right of

fixation, on the horizontal midline. On trials with an additional no-onset distracter the fifth placeholder was at the location of the upcoming extra distracter. On onset distracter trials the fifth placeholder was opposite to the location of the additional distracter. Thus, there were six positions in which elements could be presented; these six locations were arranged on the circumference of an imaginary circle around fixation with a radius of 7.3°. Placeholders were grey vertical bars subtending 0.6° x 1.9°. Placeholders and the fixation point were of the same chromaticity (CIE x,y chromaticity co-ordinates of .28/.30) and luminance (7.6 cd/m^2), and were presented on a black background (0.01 cd/m^2). The additional distracter (onset or no-onset) could appear left or right of fixation, on the horizontal midline. The search displays consisted of red (CIE co-ordinates of .63/.33) and green (CIE co-ordinates of .29/.59) vertical bars of the same size and similar luminance as the placeholders.

Displays were presented on a 17" SVGA monitor with 800 x 600 pixel resolution and 74 Hz refresh rate. The monitor was located at 57 cm from the chinrest. A second PC was used to record eye position data on-line. Eye movements were monitored with the SMI EyeLink System (SensoMotoric Instruments GmbH, Teltow, Germany). The system uses the centre of the pupil and the corneal reflection technique to define pupil position. Eye movements were recorded at 250 Hz, with an operational spatial resolution of about 0.3°. Saccade onset was defined as a change in eye position with a minimum velocity of 35 °/s or a minimum acceleration of 9500 °/s^2.

Trials on which the central disk was not properly fixated (deviation larger than 2°) at presentation of the search display, were excluded from analysis. Trials on which observers made a saccade with a latency shorter than 125 ms were considered anticipatory and were excluded from further

analysis (see also Ludwig & Gilchrist 2002). Moreover, trials with no, too small (shorter than 3°), or too large a saccade (12° or more), were rejected. Employing these criteria resulted in 3.9% of the patient's, and 11.8% of the control group's trials being rejected. A further 0.5% of the control group's trials were rejected due to recording errors or a failure to saccade.

In order to determine the landing position of the first saccade, the imaginary circle on which the display elements were positioned was divided into eight 45° segments, six of which could contain a display element. If the amplitude of the saccade was between 3° and 12°, the saccade was classified as having landed either on the target, on the additional distracter, on any of the other distracters, or in an empty display segment. Because the vast majority of saccades were directed either to the target or the additional distracter, the few saccades that landed in an empty segment or on one of the other distracter items were excluded from further analysis. This resulted in rejection of 0.9% of the control group trials. It is slightly surprising that the patient showed better performance in this respect than the control group as a whole. However the absolute number of error trials was very small and a number of controls also had rates at 0%. A similar pattern has been reported before (Kumada and Hayashi, 2005).

Procedure

Each of the four blocks of trials started with a nine-point grid calibration and validation procedure. Participants were asked to saccade to a grey, circular disk (identical to the fixation point) that appeared sequentially (but unpredictably) in a 3x3 grid. After a satisfactory validation had been obtained, a block of trials was run.

Participants searched for the red target among green distracters and signalled the target location by making a saccade to it. On each trial, an additional distracter would appear, either left or right of fixation on the horizontal midline. This additional distracter was completely irrelevant to the task and participants were instructed to ignore it. It could be either similar (identical) or dissimilar (but similar to the other distracters) to the target. In addition, it could appear either in a location previously occupied by an extra placeholder (no-onset distracter) or in a previously empty location (onset distracter). Combining the similar/dissimilar and onset/no-onset factors created four trial types: similar onset, similar no-onset, dissimilar onset, and dissimilar no-onset. These four trial types were equally distributed over the 64 trials in a block. The different trial types were randomly intermixed in each block.

In between trials a fixation display was presented, consisting of just the central fixation disk. When properly fixated by the observer, the experimenter initiated a new trial and, if necessary, an automatic spatial drift correction was performed. An experimental trial began with the 600 ms presentation of the placeholders, followed by the search display. The search display remained visible for 1 second.

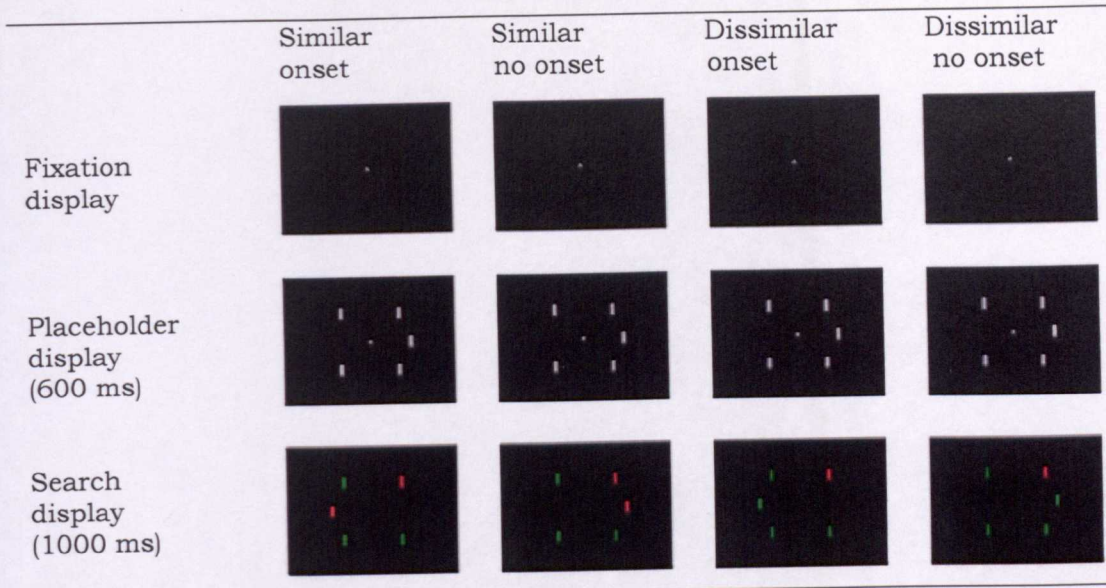


Figure 5.1: Schematic illustration of the sequence and timing of events of the different trial types. Placeholders are indicated by the gray bars. Bars that appeared in a distracter color are shown in green, and bars that appeared in the target color are shown in red.

Results

The analyses reported here focus on the extent of capture across conditions and locations. Summary statistics for the latency data are also reported, however, no formal statistical analysis of these data was carried out. This is because the very large differences in number of correct and incorrect latencies across conditions, in particular for the patient compared to the controls, did not permit calculation of a stable measure of central tendency, for each participant, in all conditions.

Overall the patient's first saccade was directed to the additional distracter on 34% of trials compared with 17% for the control participants. Table 5.1 reports the capture effect obtained for the four trial conditions (similar onset, similar no-onset, dissimilar onset, and dissimilar no-onset). Compared to the overall pattern of results in the elderly subjects, the table shows that the patient was overall more distractible, with capture occurring

more frequently in all four conditions. The pattern of oculomotor capture in the patient was, however, similar to that of the elderly control group.

Table 5.1: Proportion of oculomotor capture for TH and controls (means)

	Overall	TH				Controls overall
		left target		right target		
		left distract.	right distract.	left distract.	right distract.	
Similar onset	0.84	0.93	0.88	0.60	0.94	0.43
Similar no-onset	0.39	0.53	0.53	0.06	0.44	0.22
Dissimilar onset	0.12	0.20	0.06	0.00	0.23	0.02
Dissimilar no-onset	0.02	0.07	0.00	0.00	0.00	<0.01

The effect of the spatial position of both the target and distracter on overall capture rates for the patient were examined. Table 5.2 shows the capture effect broken down by the hemifield in which the target and distracter appeared. I first report the overall level of capture. For three of the four target-distracter location combinations, TH showed increased capture levels that were outside the 99% confidence intervals for the controls. In the fourth condition, where TH did not differ reliably from the controls, the target was on the right-hand side and the distracter is on the left. This is the situation in which one would expect to find extinction of the additional distracter, if any extinction were to occur.

In order to investigate the effect of Similarity, for each target-distracter location combination a difference score was calculated between the similar and dissimilar distracter conditions, across the Onset factor. The larger the difference in this score, the more the capture effect is modulated by the similarity to the target. Again in three of the four spatial combinations I

observed a reliable increase in the similarity effect and in the fourth combination (target right, distracter left) I again found that this effect is modulated by spatial extinction. The presence of these large effects of similarity strongly suggests that TH is able to weigh visual signals according to similarity in the colour domain. In fact, inspection of Table 5.1 reveals a more complex pattern.

In the similar no-onset conditions, the target and distracter are only distinguishable on the basis of location information: The target is the red item that appears along one of the oblique meridians, whereas the distracter appears on the horizontal meridian. In 3 out of 4 of the target – distracter location combinations, performance is very close to chance. This finding suggests that TH is able to use target similarity to guide his eye movements, but is unable to use location information alone to filter task-irrelevant visual signals.

I investigated the effect of the Onset by calculating a difference score between the onset and no-onset conditions, across the Similarity factor. The larger this score, the more capture is modulated by the distracter appearing with an abrupt onset. In all four spatial positions TH is reliably more disrupted by the onset than the control participants (see table 5.2).

Table 5.2: Capture effects (proportions of saccades on distracter) by hemifield of target and distracter

	TH			
	left target		right target	
	left distracter	right distracter	left distracter	right distracter
Overall	0.43*	0.37*	0.17	0.40*
Similar (S)	0.73*	0.70*	0.33	0.69*
Dissimilar (D)	0.13*	0.03*	0.00	0.12*
Similarity effect (S – D)	0.60*	0.67*	0.33	0.57*
Onset (O)	0.57*	0.47*	0.30*	0.58*
Noonset (N)	0.30*	0.27*	0.03	0.22*
Onset effect (O - N)	0.27*	0.20*	0.27*	0.37*

* indicates outwith 99% confidence interval of controls

	Controls			
	left target		right target	
	left distracter	right distracter	left distracter	right distracter
Overall	0.17	0.16	0.13	0.21
Similar (S)	0.33	0.32	0.25	0.39
Dissimilar (D)	0.02	0.00	0.01	0.03
Similarity effect (S – D)	0.31	0.32	0.24	0.36
Onset (O)	0.24	0.19	0.16	0.30
Noonset (N)	0.10	0.13	0.10	0.12
Onset effect (O - N)	0.14	0.06	0.06	0.18

Table 5.3 lists the mean latency of the first saccade for TH, and the average latency for the control group. On the whole, it appears that TH's saccadic reaction times were in the same range as that of the control participants. In addition, the pattern of latencies across the four conditions was similar in the patient and controls, and similar to that found by Ludwig and Gilchrist (2002; 2003a). For both the patient and the controls the saccade latencies to the additional distracter were generally shorter than those to the target. Interestingly, again the extinction like effect apparent for the saccade errors also appeared in the saccade latencies of the patient (Table 5.4). When the target was on the right and the additional distracter on the left his saccade

latencies to the target were considerably shorter than those of the control subjects.

Table 5.3. Mean saccadic reaction times for TH and average control reaction times (ms). The number of trials is given in parentheses for TH.

	TH		Controls	
	Correct	**Incorrect**	**Correct**	**Incorrect**
Similar onset	323 (10)	242 (52)	394	255
Similar no-onset	337 (38)	298 (24)	348	312
Dissimilar onset	280 (52)	207 (7)	303	268
Dissimilar no-onset	270 (62)	203 (1)	298	195

Table 5.4. Saccadic reaction times (ms) by hemifield of target and distracter

TH			
left target		**right target**	
left distract.	**right distract.**	**left distract.**	**right distract.**
Correct saccades			
303 (34)	329 (40)	266 (52)	280 (36)
Incorrect saccades			
245 (26)	267 (23)	291 (10)	238 (25)

Controls			
left target		**right target**	
left distract.	**right distract.**	**left distract.**	**right distract.**
Correct saccades			
325	336	331	319
Incorrect saccades			
272	270	308	258

Discussion

Using an adaptation of the oculomotor capture paradigm both stimulus and goal driven control of saccade target selection were studied following

damage to the temporo-parietal region. There are three key findings. First, there was an overall elevation of the extent of capture in this patient compared to controls. Second, no evidence was observed of a differential deficit in either stimulus or goal driven control. And third, an interaction was found between visual extinction and stimulus and goal driven capture.

Overall elevation of the extent of capture in this patient compared to controls.

The inability to inhibit responses to task irrelevant stimuli is classically associated with damage to the frontal lobe (Guitton et al, 1985; Everling & Fischer, 1998; Munoz & Everling, 2004). In the context of saccade generation, frontal damage impairs the ability to suppress involuntary orienting movements (Guitton et al., 1985). Interestingly, the patient in the current study has no damage to these frontal structures but still is unable to appropriately inhibit saccades to the task irrelevant distracters. One possibility is that this overall deficit is simply a result of a lack of arousal and/or motivation. Such deficits have previously been reported to affect attentional control and induce lateral biases (Robertson, Tegnér, Tham, Lo, & Nimmo-Smith, 1995). However, a number of observations argue against this possibility. First, the patient followed the instructions precisely (generally better than the controls) and never saccaded into an empty space. Second, the SRT's produced when the patient saccaded to the distracters were very short, an unlikely result had arousal indeed been low. Third, as discussed below the overall elevation in the extent of capture interacted in a complex way with the spatial location and properties of the distracter.

Instead these results suggest an additional role for temporo-parietal areas in this control function. This conclusion is consistent with a recent

attempt to characterise the attentional deficits following unilateral brain damage, using a well-established computational model of attentional functioning (Peers et al., 2005). Parameters of the model can be used to derive a measure of the quality of top-down control on the basis of behavioural relevance. Most interestingly, Peers et al. (2005) showed that although parietal and frontal patients as a group were not impaired relative to controls, patients who did show impairments were not confined to those suffering from frontal damage.

It has to be conceded though that, although the scan performed on the patient showed a discrete lesion to temporo-parietal cortex with no white matter damage, it is not possible to completely exclude the possibility that more detailed scanning procedures may have revealed frontal and white matter tract damage. However the complex interaction between the spatial deficit and the differential effects of similar and dissimilar distracters suggests even at a functional level a far more interactive and integrated system of control.

No evidence of a differential deficit in either stimulus or goal-driven control.

Inspection of Table 5.2 may suggest that the patient is more affected by similarity and onset than the age matched controls. However, it is important to be aware that the *overall* level of capture in this patient is elevated substantially in most spatial locations: rates of capture are double those observed on average in the controls. As a result it is reasonable to assume that this increase in capture rate will lead to an elevation in the difference in capture between conditions. The computation of both stimulus-driven and goal-driven salience signals occurs in the patient as, similarly to the control

participants, capture in the patient was modulated by both the onset and the similarity of the distracter to the target. This suggests that the computation of both goal-driven and stimulus-driven salience signals does take place in this patient.

In fact, the data suggest that TH's major problem may lie in goal-driven control on the basis of spatial location. The target only ever appeared in one of four locations, arranged along the major diagonals. A no-onset similar additional distracter could only be distinguished from the target because it appeared in a "nontarget" location. Under these conditions the patient's performance was close to chance. This could suggest that he had no control to prespecified target locations although, with hindsight, to investigate this precisely it would have been necessary to vary the probability of the target location. Regarding top down control of *features,* TH's data suggest that this process is largely intact as only distracters contingent to the target feature captured eye movements. Only very few erroneous eye movements were made to distracters dissimilar to the target colour.

Interaction between visual extinction and stimulus and goal driven capture.

Although levels of capture were elevated overall there were important spatial modulations of this effect. Despite not showing evidence of extinction on a computerised clinical assessment task, TH showed an extinction like phenomenon here: when the target was ipsilesional and the distracter contralesional the extent of capture was dramatically reduced. However, most interestingly the difference between onset and no-onset distracters is the same in the right and left visual field. This suggests that a) the onset based processing occurs before the influence of the spatial deficit that leads to the

extinction, and b) that the similarity based processing occurs after the spatial deficit. Previous studies have shown that perceptual grouping processes occur before the spatial deficit and so can reduce the extent of extinction (e.g. Gilchrist, Humphreys & Riddoch, 1996). Further onset-based capture occurring before the spatial deficit, is very much in line with a recent study by Humphreys, Olivers, & Yoon (2006), who report the sparing of onset capture in both contra- and ipsilateral visual fields in patients with inferior parietal damage. This does not necessarily imply that the two types of influence on capture are not combined at a later stage of processing. Indeed work on saccade curvature (Ludwig & Gilchrist, 2003b) suggests that these two types of information are eventually combined to calculate a single measure of salience.

The present results indicated elevated levels of capture in a patient with a temporo-parietal lesion. It would appear that, at least in the oculomotor domain, successful inhibition of task irrelevant information requires intact functioning of posterior cortical areas. These results then provide evidence for a more integrated view of the functioning of the parietal-frontal network responsible for saccadic orienting. In addition I report evidence for an interaction between spatial extinction and the factors driving capture. Stimulus-based factors have an influence before the spatial deficit and goal-based factors have an influence after the spatial deficit.

Together these results support the view that information from different stages in the processing hierarchy feed into a common functional salience map that in turn determines the distractibility of stimuli in the environment. They are in line with recent neuro-imaging data (Serences et al, 2005) implicating temporo-parietal structures (together with frontal areas) in co-ordinating goal and stimulus driven attentional control settings. However, the present

conclusions would be stronger were it possible to display the same performance deficits in larger groups of patients, and to this end I shall turn to an examination of the performance of both cortical and sub-cortically lesioned patients.

Experiment 6: Impairments of goal and stimulus driven control in patients with right hemisphere subcortical and posterior cortical lesions

Method

Healthy participants

The same twelve elderly control subjects outlined in the preceding case study took part in the experiment and were reimbursed for travel expenses.

Patients

6 patients with sub-cortical lesions (mean age, 61.5, SD 9.6) and 7 patients with cortical lesions (mean age 64.6, SD 9.6) were included in the study. Lesion details and chronicity for cortical and sub-cortical patients can be seen in tables 6.1 and 6.2, whilst lesion maps can be seen in figures 6.1 and 6.2. The study was conducted in accordance with the ethical guidelines of the South Glasgow University Hospitals NHS trust and the Declaration of Helsinki. All participants gave their informed consent prior to the study.

Colour vision

All participants[1] were screened with a short version of the Ishihara Tests for Colour Blindness (Ishihara, 1968) to ensure they could discriminate the colours used in the experiment. All healthy adult controls passed. Sub-cortical patient GM failed the Ishihara test but was able to correctly identify the colours of the rectangle stimuli on the paper instructions and was thus included in the study, JQ failed one plate out of 6, MK, LM, AA and BM passed. For cortical patients, JM initially failed one plate possibly due to neglect but correctly identified when re-asked, TH, JC, JS, HM and JB passed.

Apparatus and stimuli

Apparatus, stimuli and procedures were as described in experiment 5. Trial exclusion criteria of improper fixation, anticipation or amplitude magnitude also matched those employed in experiment 5[2]. These criteria resulted in rejection of 20.8% of the patient, and 11.8% of the control group trials. A further 0.5% of the control group data was rejected due to recording errors or a failure to saccade, whilst 2.2% of the patients trials were rejected for technical failures, failure to saccade or failure to follow task instructions.

Also in line with experiment 5, because the vast majority of saccades were directed either to the target or the additional distracter, the few saccades that landed in an empty segment or on one of the other distracter items were excluded from further analysis. This resulted in rejection of 0.9% of the

[1] Patient JHH unfortunately was not tested, but it can be seen from results that her performance in the study was in line with that of the control group

[2] These criteria were relaxed for patient JM, as he had some difficulty performing the task and was also difficult to track. His first block was discarded due to failure to follow task instructions. The anticipation criteria was reduced to 100ms, improper fixation extended to 3 degrees and the amplitude criterion was discarded (his range was 1.7 to 16.3 degrees). Still, only 68 trials were subsequently included in the analysis.

control group trials, 4.3% of the cortical groups trials, and 6.6% of the sub-cortical groups trials.

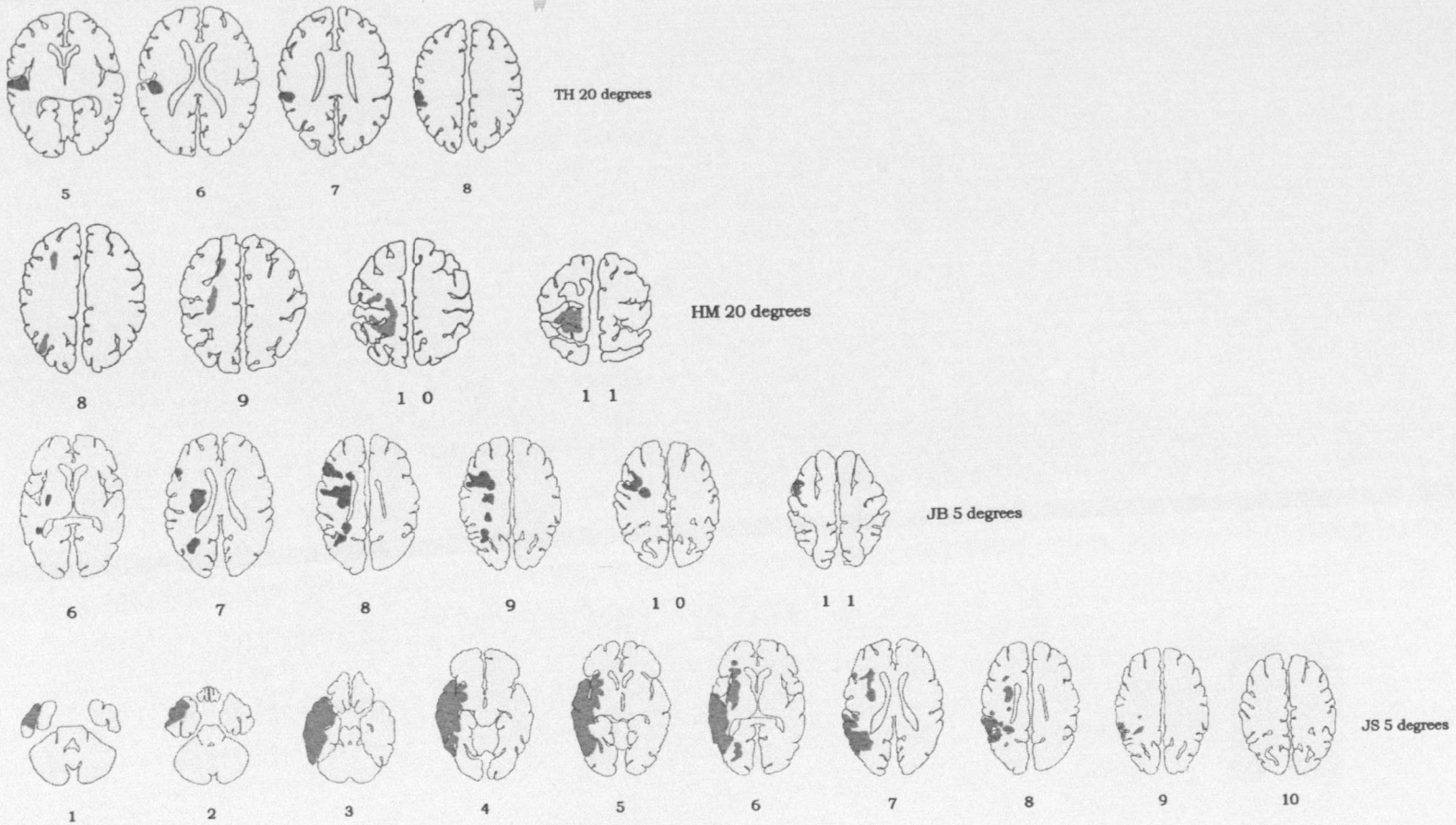
Table 6.1: Lesion and chronicity details for cortical patients

Patient	Lesion chronicity (months)	BIT score (<130 fail)	Lesion	Lesion details: Cortical patients
TH	15	129	Infarct	Temporo-parietal.
JC	3	93	Infarct	Superior post-central gyrus (parietal lobe) and occipital cortex.
JHH	4	137	Infarct	Frontal.
JS	6	117	Infarct	Temporal lobe, insular cortex.
JM	11	61	Infarct	Frontal cortex, basal ganglia.
HM	9	132	Infarct	Parietal cortex, superior part post central gyrus.
JB	7	139	Infarct	Lentiform nucleus, posterior frontal cortex.

Table 6.2: Lesion and chronicity details for sub-cortical patients

Patient	Lesion chronicity (months)	BIT score	Lesion	Lesion details: Sub-cortical patients
GM	13	141	Infarct	Centrum semiovale.
MK	15	144	Haematoma	Thalamic.
LM	16	135	Infarct	Thalamic, internal capsule.
JQ	4	35	Haematoma	Basal ganglia.
AA	1	146	Haematoma	Basal ganglia, extending into posterior insular cortex.
BM	5	144	Haematoma	Basal ganglia, insula.

Figure 6.1 Cortical patients lesion maps. Templates were taken from Damasio and Damasio, 1989



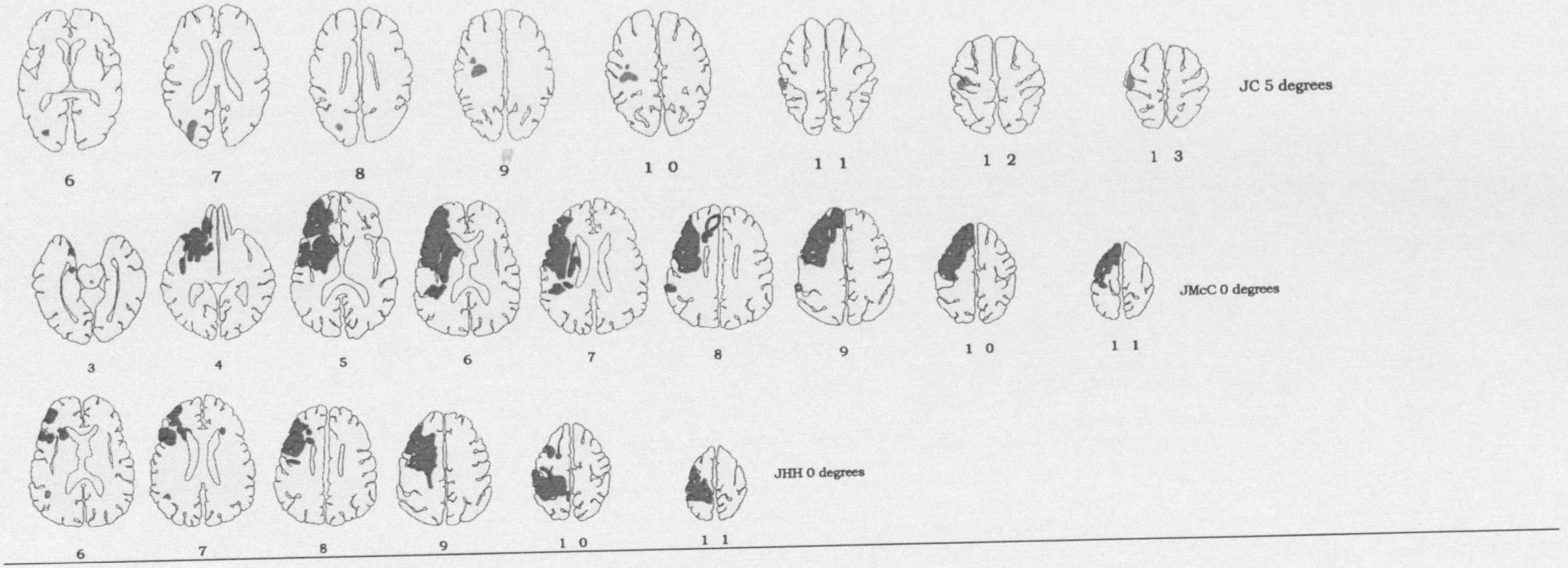
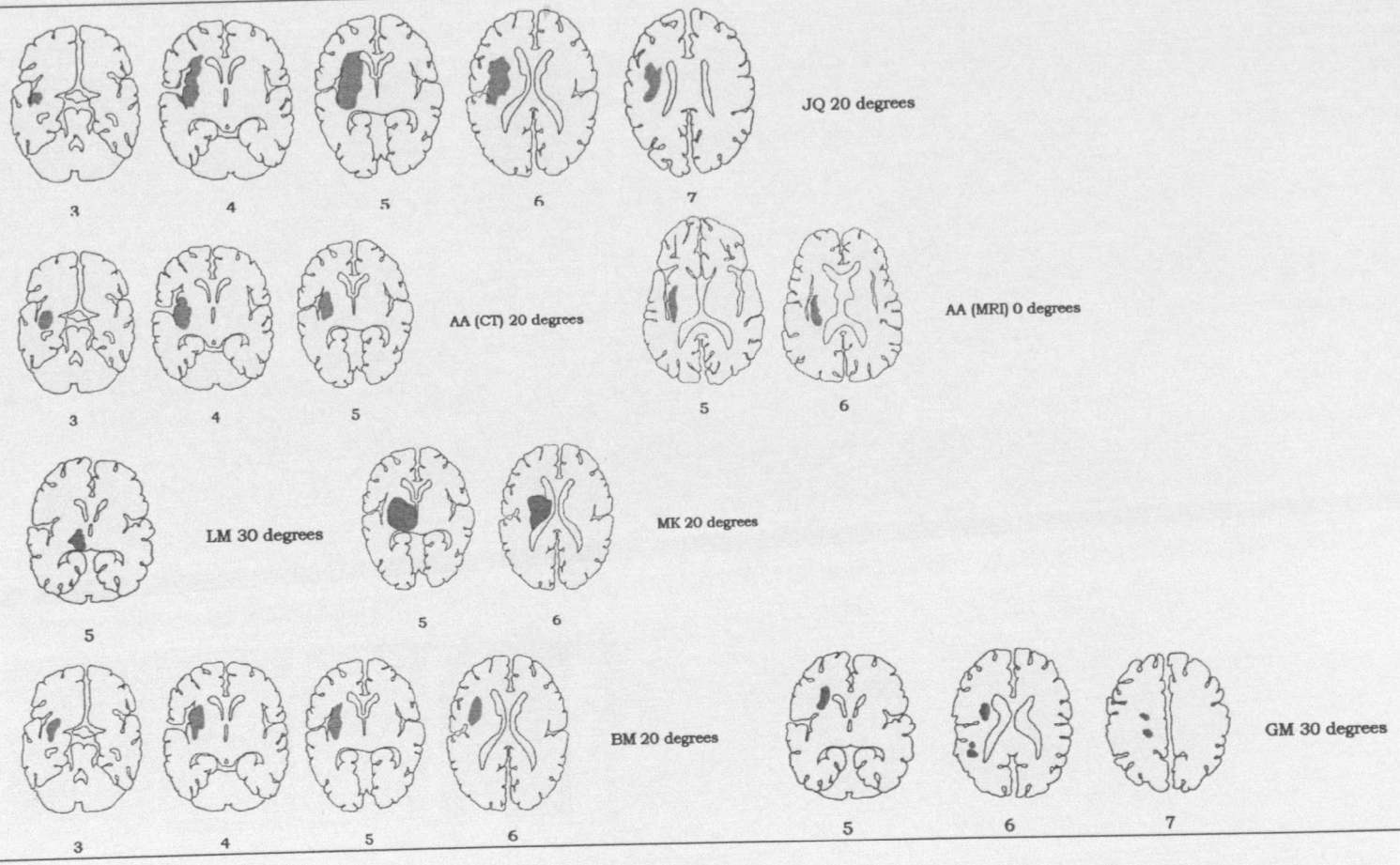

6
7
8
9
1 0
1 1
1 2
1 3
JC 5 degrees
3
4
5
6
7
8
9
1 0
1 1
JMcC 0 degrees
6
7
8
9
1 0
1 1
JHH 0 degrees

Figure 6.2 Sub-cortical patients lesion maps. Templates were taken from Damasio and Damasio, 1989



Results

Capture

Over all trials, the healthy control group's first saccade was directed to the additional distracter on 17% of trials, compared to 26% for the cortical patient group and 25% for the sub-cortical patient group.

Ludwig & Gilchrist (2002) reported that the effect of capture on the additional distracter was particularly pronounced when the additional distracter was similar to the target, especially when it appeared with a sudden onset. To examine the performance of the participants, I first calculated for each subject the percentage of first saccades that went to the additional distracter rather than the target separately for cases when the additional distracter was similar or dissimilar to the target, and appeared either with or without a sudden onset. The overall pattern of results in the elderly subjects was highly similar to that reported by Ludwig and Gilchrist (2002; 2003a) for a younger group of participants. That is, the irrelevant distracter was frequently fixated, particularly if it appeared in the target colour and with an abrupt onset.

Table 6.3: Overall mean percentage of first saccades directed to the additional distracter rather than the target for similar onset, similar no-onset, dissimilar onset and dissimilar no-onset conditions across subjects for all three groups.

	Similar onset	Similar no-onset	Dissimilar onset	Dissimilar no-onset
Controls	43%	22%	3%	<1%
Cortical group	61%	28%	20%	1%
Sub-cortical group	59%	26%	23%	4%

With regard to group comparisons of performance in the task, overall means for all three groups for all 4 conditions can be seen in table 6.3. It can be seen

here that the two patient groups appeared to be broadly in line with the control group for conditions were the additional distracter appeared without a sudden onset. In these conditions the percentage of first saccades directed to the additional distracter rather than the target was similar. A different pattern emerged when the additional distracter appeared with a sudden onset however, here both patient groups were particularly prone to the effects of the distracter.

To examine group differences further a 2x2x3 mixed ANOVA with within factors of Onset and Similarity and a between factor of Group (controls, cortical patients and sub-cortical patients) was conducted (this dataset did not meet the assumption of homogeneity, although this was correctable with root transformations of the data which were therefore employed in the ANOVA). Main effects were revealed of Similarity ($F(1,22)=205.22$, $p<.001$) and Onset ($F(1, 22)=79.42$, $p<.001$).

Thus the results reported here indicate that similar distracters have a stronger distracting effect than dissimilar distracters, with similar onsets being more distracting than similar no-onsets. Ludwig and Gilchrist (2002, experiment 2) obtained similar main effects of similarity and onset and reported with post hoc comparisons that similar onsets were more distracting than dissimilar onsets. A similar difference was observed when I made the same pairwise comparison with the present results ($p<.001$). Ludwig and Gilchrist further reported that similar onsets captured the eyes more frequently than similar no-onset distracters, a pattern that was repeated when the same pairwise comparison was made with the present data ($p<.001$).

Additionally, a main effect of Group was revealed ($F(2,22)=5.40$, $p<.05$), as was a significant interaction between Group and the factor of Onset ($F(2,22)=3.58$, $p<.05$). With regard to the main effect of Group, pairwise

comparisons indicated that the cortical and subcortical groups had significantly higher error rates than the control group (both $p<.05$), whilst the error rates of the two patient groups did not differ from each other ($p=1.00$). Examination of the interaction of Group and Onset revealed significant group differences only in the condition where the distracter appeared with a sudden onset. In this condition the error rate of the cortical group of patients was significantly higher than the control group ($p<.05$), whilst a trend to a similar pattern was observed when comparing the error rate of the subcortical group of patients to the control group ($p=.06$). No other factors or interactions revealed significant (or near significant) effects.

In order to examine any possible effects of the lateralisation of the target and the distracter on the degree of overall capture, a mixed ANOVA on the percentage of first saccades made to the additional distracter rather than the target, with within subjects factors of Target Side (left or right) and Distracter Side (left or right), and between subjects factor of Group (control, cortical and sub-cortical group), was conducted (again this dataset did not meet the assumption of homogeneity, although this was correctable with root transformations of the data which were therefore employed in the ANOVA). Mean scores can be seen in table 6.4.

Table 6.4: Mean percent of first saccades made to the additional distracter rather than the target for left and right targets and distracters.

Condition	Control group	Cortical group	Subcortical group
Left target, left distracter	18%	35%	37%
Left target, right distracter	16%	35%	37%
Right target, left distracter	13%	12%	20%
Right target, right distracter	22%	31%	28%

Analysis of the ANOVA revealed significant main effects of Target Side ($F(1,22)=19.28$, $p<.001$) and a significant interaction between Target Side and Group ($F(2,22)=6.94$, $p<.01$), pairwise comparisons of this interaction revealed significant differences for left target's only between controls and sub-cortical's ($p<.05$) and also a significant difference for left targets only between controls and corticals ($p<.05$), no significant difference was revealed between cortical and sub-cortical patient groups. Additionally, this analysis revealed significant differences between capture levels for left and right targets for both cortical patients and sub-cortical patients (both $p<.01$), with higher levels of capture by the additional distracter for left targets, this was not the case for controls.

Additionally a significant main effect of Distracter Side was revealed ($F(1, 22)=6.30$, $p<.05$) as was an interaction between Target Side and Distracter Side ($F(1,22)=31.66$, $p<.001$). A breakdown of this interaction revealed significant differences between capture levels by the additional distracter between left and right distracters when the target was on the right side only (with right sided distracters more distracting, $p<.001$), and a significant difference between capture levels for the additional distracter between left and right targets when the distracter was on the left side only ($p<.001$). However, these effects did not involve any group differences. No other significant main effects or interactions were observed.

Saccadic Reaction Times

Mean saccadic reaction times for correct and incorrect trials for all three groups can be seen in table 6.5.

Table 6.5: Mean saccadic reaction times (ms) for correct (on target) and incorrect (on additional distracter) trials for controls, cortical and sub-cortical groups.

	Control group	Cortical group	Sub-cortical group
On target	328	277	282
On additional distracter	290	245	241

Interestingly, it would appear that both patient groups were faster than the healthy Control group in both correct and incorrect trials. A repeated measures ANOVA with within subject factor of Accuracy (first saccade to target or additional distracter) and between subjects factor of Group (control, cortical or sub-cortical groups) however revealed only a main effect of Accuracy, with faster saccades made by all groups in incorrect trials ($F(1,22)=25.9$, $p<.001$).

Saccadic reaction times to targets in correct trials and additional distracters in incorrect trials were calculated for each group for similar onset, similar no-onset, dissimilar onset and dissimilar no-onset conditions, mean results can be seen in table 6.6.

Table 6.6: Mean saccadic reaction times in milliseconds to targets in correct trials and additional distracter in incorrect for each group for similar onset, similar no-onset, dissimilar onset and dissimilar no-onset conditions, (*N*) = no. of trials.

	Similar onset	Similar no-onset	Dissimilar onset	Dissimilar no-onset
Control group				
On target	*(385)* 381 ms	*(514)* 349 ms	*(644)* 309 ms	*(670)* 300 ms
On additional distracter	*(292)* 276 ms	*(147)* 329 ms	*(16)* 275 ms	*(2)* 195 ms
Cortical group				
On target	*(124)* 314 ms	*(227)* 290 ms	*(273)* 260 ms	*(323)* 263 ms
On additional distracter	*(196)* 241 ms	*(88)* 249 ms	*(54)* 234 ms	*(3)* 229 ms
Sub-cortical group				
On target	*(131)* 315 ms	*(217)* 296 ms	*(242)* 270 ms	*(259)* 267 ms
On additional distracter	*(163)* 231 ms	*(67)* 255 ms	*(42)* 244 ms	*(8)* 280 ms

It can be seen that the pattern of higher latencies for correct trials continues. However, as in the single case report, no formal statistical analysis of these data was carried out. This is because the very large differences in number of correct and incorrect latencies across conditions, with some subjects having very low numbers of trials in some cells, did not allow the calculation of a stable measure of central tendency, for each participant, in all conditions.

Confidence interval analysis

As a further comparison between patient and control groups, confidence interval analyses were performed on the results. Firstly, confidence intervals were calculated based on the per subject mean percentage of first saccades made to the additional distracter rather than the target collapsed across both Similarity and Onset conditions to obtain a measure of overall oculomotor capture for the control group and the patient groups. From the data of the control group a confidence interval was calculated, two tailed, at 99% significance. Control group and individual patient performance can be seen in table 6.7 and figure 6.3.

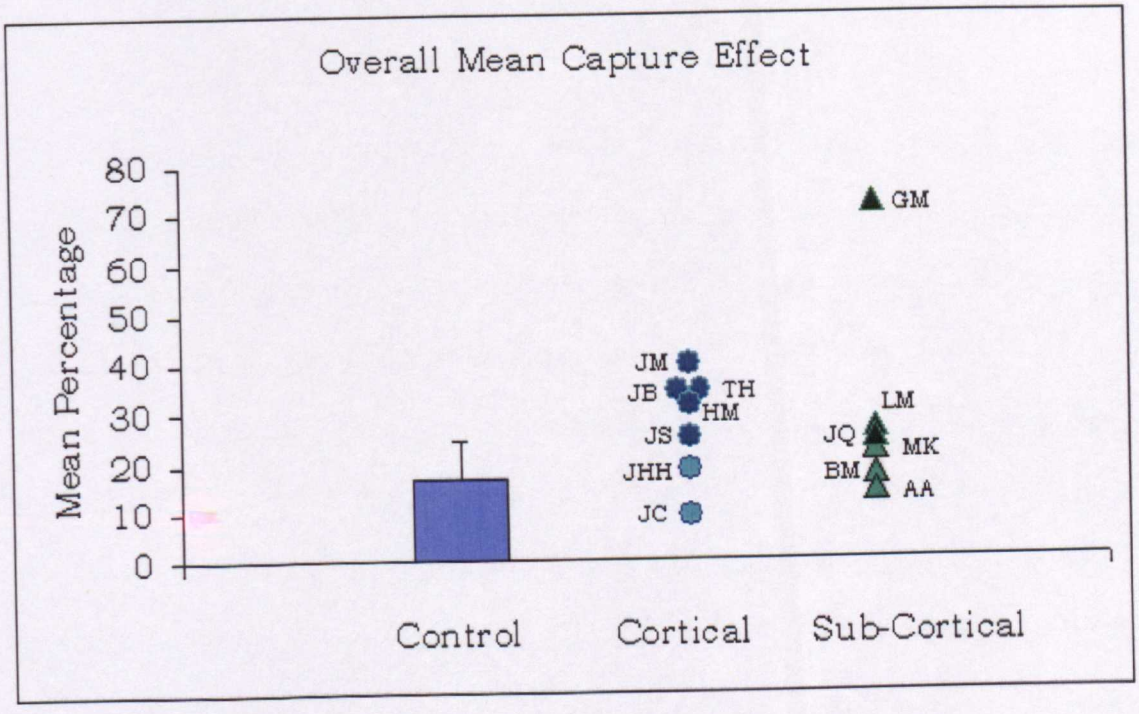


Figure 6.3: Overall mean oculomotor capture by the additional distracter for control group, cortical group and sub-cortical group, with confidence interval of control group shown.

Table 6.7: Overall mean oculomotor capture by the additional distracter for control group, cortical group and sub-cortical group (asterisks indicate outwith CI).

Group		Percentage of overall capture by additional distracter
Control group	Mean	16.95
	99% CI	9.60 - 24.30
Cortical group	JC	9.04
	JHH	18.20
	TH	34.15*
	JM	39.71*
	JS	24.87*
	JB	34.27*
	HM	31.45*
Sub-cortical group	BM	17.21
	MK	22.61
	AA	14.23
	GM	72.04*
	LM	26.94*
	JQ	24.83*

Here it can be seen that the degree of overall capture for the majority of the cortical group of patients is outwith the 99% confidence interval of the control group and that half the sub-cortical group of patients indicate a performance level out with this interval.

Next, in order to examine the effect of Similarity of the additional distracter through confidence interval analysis, a mean difference score between the similar and dissimilar distracter conditions, across the factor of Onset, was calculated for the control group. The larger the difference in this score, the more the capture effect is modulated by the similarity to the target. From the data of the control group a confidence interval was calculated, two tailed, at 99% significance. Control group and individual patient performance can be seen in table 6.8 and figure 6.4.

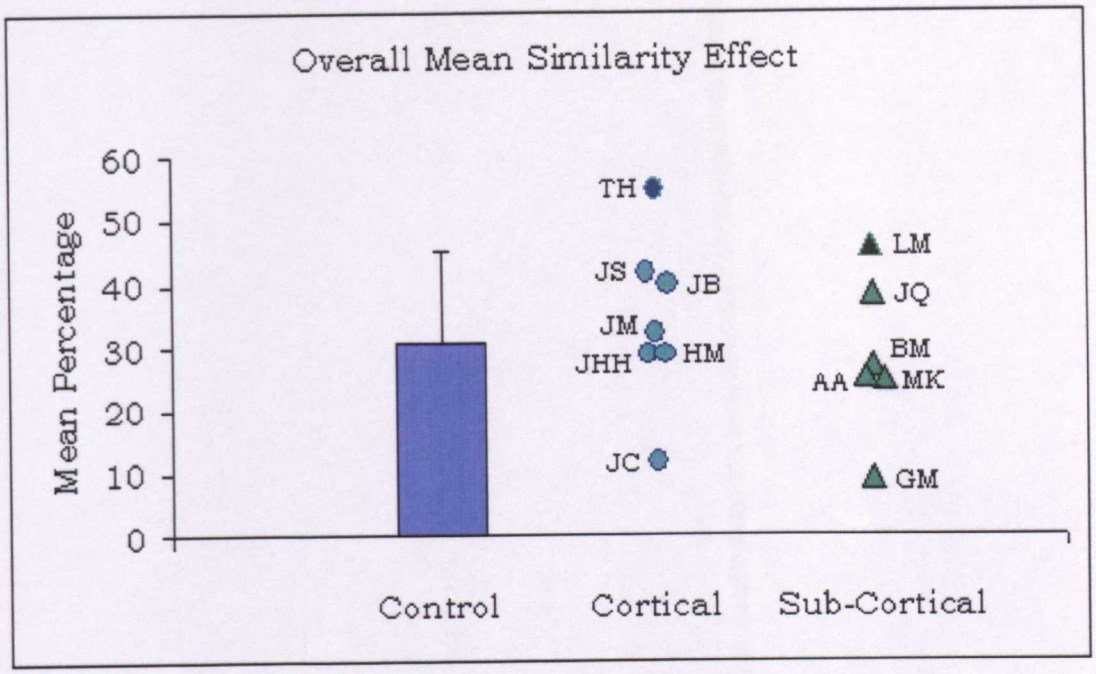


Figure 6.4: Overall mean similarity effect of the additional distracter for control group, cortical group and sub-cortical group, with confidence interval of control group shown

Table 6.8: Overall mean similarity effect of the additional distracter for control group, cortical group and sub-cortical group (asterisks indicate outwith CI).

		Percentage score of similarity effect
Control group	Mean	30.96
	99% CI	16.85 - 45.07
Cortical group	JM	32.35
	JS	41.79
	JC	11.58
	JHH	28.93
	JB	40.05
	HM	29.01
	TH	54.73*
Sub-cortical group	BM	27.14
	MK	24.92
	AA	25.41
	GM	9.26
	JQ	38.45
	LM	45.88*

Here it can be seen that only one patient from both the cortical patient and the sub-cortical patient groups display a performance that is out with the 99%

confidence interval of the control group. The cortical patient indicated here is patient TH referred to in the single case study.

Finally, in order to examine the effect of Onset of the additional distracter through confidence interval analysis, a mean difference score between the onset and no-onset distracter conditions, across the factor of Similarity, was calculated for the control group. The larger the difference in this score, the more the capture effect is modulated by the onset of the target. From the data of the control group a confidence interval was calculated, two tailed, at 99% significance. Control group and individual patient performance can be seen in table 6.9 and figure 6.5.

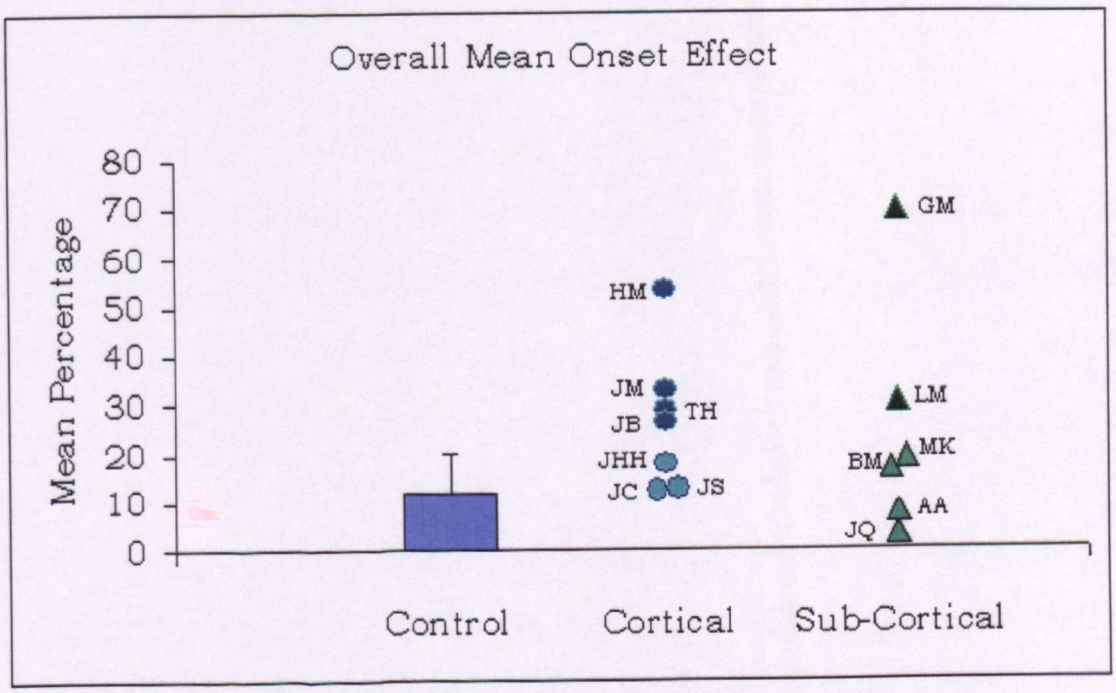


Figure 6.5: Overall mean onset effect of the additional distracter for control group, cortical group and sub-cortical group, with confidence interval of control group shown

Table 6.9: Overall mean onset effect of the additional distracter for control group, cortical group and sub-cortical group (asterisks indicate outwith CI).

Group		Percentage score of onset effect
Control group	99% CI	3.18 - 20.20
	MEAN	11.69
Cortical group	JS	12.69
	JC	12.11
	JHH	17.79
	TH	28.76*
	JM	33.16*
	JB	26.32*
	HM	53.30*
Sub-cortical group	BM	16.88
	MK	19.13
	AA	8.02
	JQ	3.10
	GM	69.70*
	LM	30.81*

These findings would indicate a tendency for onset based capture to be more disruptive in the cortical group compared to the sub-cortical group by a slight margin, although members of both groups fall outwith the control groups confidence interval.

Discussion

The allocation of visual attention can be either stimulus or goal-directed, in that it may be directed on the basis of image properties alone or be fully controlled by the nature of the observer's goals (Egeth & Yantis, 1997). The performance of healthy older adults, and patients with cortical and sub-cortical right hemispheric lesions was examined in an oculomotor capture task adapted from the paradigm employed by Ludwig and Gilchrist (2002). Across all three groups, a consistent effect of capture by the distracter was found in a large proportion of trials. Even for healthy participants the additional

distracter was found to capture the eyes on 17% of all trials. In fact deserving of comment was the remarkable consistency of the effect of capture in this older group compared to that reported by Ludwig and Gilchrist (2002) for groups of younger adults, with highly similar effects found of similarity and onset in the present group of healthy older adults compared to those reported by Ludwig and Gilchrist (2002, experiment 2).

This result is in some ways surprising, given the evidence that older adults can display increases in distractibility in similar tasks (Olincy et al, 1997; Pratt and Bellomo, 1999; Lincort et al, 1997). However other studies of oculomotor capture have reported equivalent performances between age groups (Kramer, Hahn, Irwin, & Theeuwes, 1999; 2000).

However, it is satisfying in terms of the robustness of the effect initially reported by Ludwig and Gilchrist (2002) particularly, when, from a psychophysical point of view it is known that colour ratio differences required to obtain equiluminance differ in older adults compared to younger adults, with older adults also showing reductions for sensitivity to luminance contrasts (Fiorentini, Porciatti, Morrone and Burr, 1996).

The main effects shared by the present study and that of Ludwig and Gilchrist is that of the increased distractibility of the sudden onset additional distracter compared to the no-onset distracter, particularly when the sudden onset distracter shares the target colour. Thus in the present study I have successfully provided evidence for stimulus and goal driven capture within a single paradigm. Additionally, in line with Ludwig and Gilchrist (2002) I have demonstrated that saccadic latencies are lower for correct trials were the first saccade was made to the target, compared to incorrect trials were the first saccade was made to the additional distracter, across all three groups. This finding is also in line with Theeuwes et al (1999), who reported that when their

subjects eyes moved towards the abrupt onset distracter rather than the target that the latency to the distracter was lower than that of eye movements to the target.

Additionally, with regard to error percentage rates, in the main analysis of group onset and similarity differences I reported a significant group difference in error rate overall between healthy controls and both cortical and sub-cortical patients, in terms of the degree of distractibility of the additional distracter, with both patient groups indicating increased overall distractibility. However this finding was tempered by an interaction between the factor of group and onset which indicated a significantly stronger effect of the sudden onset of the distracter on the cortical group of patients compared to the control group, and a strong trend for the same pattern in the comparison between the subcortical group and the control group. Therefore, whilst overall attentional capture was modulated by both the similarity and onset features of the additional distracter across groups, relative to the healthy control group, the patient groups and the cortical group in particular were additionally prone to distraction in conditions where the distracter appeared with a sudden onset relative to conditions where the additional distracter appeared without a sudden onset.

To enhance the group comparisons, individual analysis of patient performance, by means of comparison to control group confidence intervals was also conducted. This indicated that the majority of the patients (particularly from the cortical patient group) had a performance profile that was outwith the confidence interval of the control group with regard to overall capture by the additional distracter. Additionally, over half of the cortical patient group, and two patients from the sub-cortical group had a performance profile in terms of mean capture by the additional distracter that

lay outside the confidence interval of the control group for capture by onset based distracters collapsed across similarity.

The evidence of significant group differences in oculomotor capture by the additional distracter is in keeping with the report by Mapstone et al (2003) of reductions in contralesional target identification and fewer fixations into contralesional hemispace demonstrated by patients with right hemisphere cortical lesions even in the absence of clinically observable neglect, and further evidence reported by Fimm et al (2001) of impairments in contralesional information processing in patients with right hemisphere sub-cortical lesions, even without neglect being present. However, with regard to contralesional search impairment, an examination of the performance of the control and patient groups with regard to lateralisation of target and distracter indicated, compared to the control group, significantly higher degrees of capture by the additional distracter when the target was on the left side, regardless of distracter side for both the cortical and subcortical group. Thus this finding of impaired search performance for contralesional targets is in line with a large corpus of research indicating impaired contralesional search in patients with right hemisphere lesions.

Additionally, an examination of table 6.4, which shows the percentages of oculomotor capture by the additional distracter broken down by target and distracter side indicates that capture was mildest in the right target-left distracter condition, and thus in line with the performance of patient TH in the preceding single case study, an extinction like effect is clearly suggested here. Results of the statistical analysis were however made somewhat indistinct by the lack of a target side by distracter side by group interaction. However, an examination of the means indicates that this was likely to be due to the fact

that the control group also showed a (smaller) drop in the degree of capture in the right target-left distracter condition.

However, the nature of the task required of the participants presents something of an interpretive dilemma, namely that the task required a visual search for a colour target and additionally required the participants to inhibit a response to an additional distracter. Impairments in the patient groups could be interpreted as either impairment in search or impairment in the patients' ability, relative to the control group, in inhibiting a response (in this case an eye movement) to the additional distracter. The performance of the patient groups was not demonstrated to differ from the controls with regard to the finding that across groups the additional distracter had a more profound impact on search performance when it shared the target colour and appeared with a sudden onset. However, overall capture rates for the patient groups were observed to be significantly higher. Additionally, the effect of the additional distracter when it appeared with a sudden onset was found to be significantly higher in the cortical patient group (and analysis indicated a similar trend in the subcortical patient group). These latter findings indicate that the patients were more distractible by sudden onsets than the control group with regard to their search performance.

All the patients studied in the present sample had posterior damage, with only some patients lesions incorporating more frontal damage. The inability to inhibit responses to task irrelevant stimuli is classically associated with damage to the frontal lobes. Guitton et al (1985) for example demonstrated difficulties in patients with frontal lobe damage in the suppression of incorrect pro-saccades in the antisaccade task. Also, goal-driven selection is deemed to depend on frontal structures (Everling & Fischer, 1998; Munoz & Everling, 2004).

Pierrot-Deseilligny and colleagues (Pierrot-Deseilligny, Milea, Muri and Rene, 2004; Pierrot-Deseilligny, Muri, Nyffeler and Milea, 2005), in recent reviews, describe the role of the human dorsolateral prefrontal cortex with regard to the preparation of saccades, and report that the inhibition of future responses is one of the key principles of prefrontal cortical function. With regard to eye movements, Pierrot-Deseilligny et al review evidence implicating lesions of the dorsolateral prefrontal cortex in error rates in antisaccade studies, and thus that this region controls the inhibition of reflexive saccades in the antisaccade task, whilst the frontal eye fields control correct antisaccades in this type of task. They conclude that the dorsolateral prefrontal cortex controls the inhibition of reflexive saccades when the parietal eye fields elicit such saccades. It is likely that dorsolateral prefrontal cortex inhibition of reflexive saccades acts directly on the superior colliculus.

However, with regard to the present results, I have observed error rates that are significantly higher than those of controls in a group of patients which include individuals without frontal lobe involvement, and indeed the individual confidence interval analysis show significant impairments in individual patients, such as TH, JS or HM, whose cortical involvement spares the frontal lobe.

Mort et al (2003) have recently used event related fMRI to examine cortical activity during both voluntary (directed by an arrow cue) and reflexive (directed by a change in luminance) saccades in healthy subjects. Reviewing previous evidence, they report that studies to date have identified three critical brain areas in generation of reflexive and voluntary saccades, the frontal eye fields (FEF), supplementary eye fields (SEF) and intra parietal sulcus (IPS) of the posterior parietal cortex (PPC) (or parietal eye field, PEF), with activations

shown in these areas for both types of saccade. However, they point out that previous research has not directly compared both types of eye movement.

When voluntary saccades were examined, relative to activation for reflexive saccades, Mort et al reported bilateral activation of both FEF and IPS, and thus that their finding is in agreement with previous literature that the FEF is involved in voluntary saccadic programming. When activity for reflexive saccades, relative to voluntary saccades were examined, Mort et al reported no evidence of activity of the FEF being greater for reflexive compared to voluntary saccades. However, activations were reported in the precuneus, posterior cingulate cortex, and angular gyrus of the inferior parietal lobule. The authors point out that the latter finding, which was strongest in the right hemisphere, thus implicates an area as more dominant for reflexive saccades compared to voluntary ones and is also classically implicated as a prime seat for lesions resulting in hemispatial neglect. Mort et al argue that this implicates the angular gyrus of the inferior parietal lobule in reflexive saccadic orienting to a target, and support a view that damage that results in neglect disrupts neural activity required for normal reflexive visual exploration.

Thus it would appear that frontal structures are vital for the suppression of unwanted and the initiation of wanted saccades, whilst reflexive saccade generation is more dependent on posterior structures such as the parietal eye fields. The results of the present study indicated error rates representing significantly higher distractibility in a group of patients, which included individuals without frontal lobe involvement. Furthermore, a subsequent confidence interval analysis indicated significant impairments of oculomotor response suppression in individual patients whose cortical lesion spared the frontal lobe. Reflexive saccade generation is clearly not impaired in these patients, rather it appears to be significantly over activated.

The human parietal eye field, which has projections to both the superior colliculus and the frontal eye fields, corresponds to the monkey lateral intraparietal area (Pierrot-Deseilligny, Milea, Muri and Rene, 2004; Grefkes and Fink, 2005). Muri, IbaZizen, Derosier, Cabanis and Pierrot-Deseilligny (1996) were the first to employ fMRI with healthy subjects in a saccade task in order to locate the human parietal eye fields. They describe the location as in the horizontal part of the deep region of the intraparietal sulcus (Brodmann areas 39 and 40), where saccade specific activity was identified. When the connections from parietal eye fields to the colliculus are damaged, Pierrot-Deseilligny et al cite earlier work (Pierrot-Deseilligny, Rivaud, Gaymard and Agid, 1991) which indicates that the PEF is fundamentally important for the generation of reflexive saccades.

Pierrot-Deseilligny, Rivaud, Gaymard and Agid (1991) studied patients with unilateral lesions to posterior parietal cortex, prefrontal cortex, frontal eye fields and the supplementary motor area in both pro- and anti-saccade tasks. Bilateral increases in saccadic latencies were reported for the group with lesions to the right posterior parietal cortex in the prosaccade task, relative to controls. Such increases were observed in the group with lesions to left posterior parietal cortex, although less profoundly and only contralesionally. No significant effects were found with regard to latencies in the groups with frontal lesions. The group with lesions to prefrontal cortex, however, were differentiated from the controls in terms of the proportion of errors made in the antisaccade task, in this task the group with lesions to posterior parietal cortex did not differ from controls. Pierrot-Deseilligny et al thus argued that the posterior parietal cortex is involved in the initiation of reflexive saccades to visually guided targets.

Indeed, the role of more posterior structures in the computation of behavioural relevance, regardless of the source of that relevance, has also been demonstrated in single-cell recordings in the monkey lateral intraparietal area (LIP; Gottlieb & Goldberg 1999; Kusunoki, Gottlieb & Goldberg, 2000). Gottlieb, Kusunoki and Goldberg (1998), for example, tested the response of LIP neurons to stimuli that entered the receptive fields by saccades. They found that neurons showed little or no response unless the stimuli were behaviourally significant. Behavioural significance was dictated either by goal-driven or stimulus-driven factors, either by making the stimulus task relevant, or by using the attraction of an abruptly appearing stimulus. From this and other related data Goldberg and colleagues argue that LIP neuronal responses are critically dependent on salience regardless of the source of that salience. Importantly, salience can be either extrinsic (produced by an abrupt onset) or dictated by the behavioural context.

Indeed Toth & Assad (2002) investigated whether LIP would encode colour if colour was behaviourally linked to the eye movement. Monkeys were trained to make an eye movement in one of two directions based alternately on the colour or location of a visual cue. When the colour was relevant for directing eye movements, a substantial fraction of LIP neurons selective for cue colour were found. However, when cue location was relevant, colour selectivity was virtually absent from LIP. This supports the notion that LIP can directly encode stimulus characteristics (even colour) if they are relevant for guiding eye movements.

Therefore, although the current data do not rule out the importance of the frontal lobe for the inhibition of task irrelevant responses, such as saccades, they support a view in which the frontal and parietal lobes together form a network that derives salience from a variety of sources, and selects

targets for goal related action. This is in keeping with a ventral right hemispheric attentional network postulated by Corbetta & Shulman (2002). They argue that this network, which includes the temporoparietal junction and the ventral frontal cortex, is involved in the direction of attention to behaviourally relevant sensory stimuli outwith the online focus of processing, possibly acting as an exogenous orienting system. They argue that attentional orienting is controlled by two systems which interact, a bilateral intraparietal sulcus-frontal eye field system is involved in top down control of visual processing whilst the right lateralised temporo-parietal junction-ventral frontal cortex system is conversely related to stimulus driven control. They postulate that connections between the temporoparietal junction and intraparietal sulcus can interrupt processing when behaviourally relevant and currently unattended stimuli are detected by the system, with the intraparietal sulcus informing the ventral attentional network with regard to the behavioural relevance of stimuli.

Related to this Snow and Mattingley (2006) have argued that right hemisphere damage can result in an imbalance between goal and stimulus driven signals in the computation of salience, resulting in ipsilesional distractibility. They recently report the results of a flanker task which they conducted to follow the work of Danckert, Maruff, Kinsella, Graaff and Currie (1999).

Danckert et al (1999) studied implicit processing of sensory information in a patient with a neglect inducing right tempero-parietal-occipital lesion. They employed a flanker task, were subjects were presented with a central letter stimulus and an irrelevant flanker letter, which subjects were told to ignore, and which could be either congruous or incongruous with regard to colour or letter. The task was simply to identify the central letter in one

condition and identify the colour in another. When controls were asked to identify the letter, only this aspect of the flanker interfered with latencies. This pattern of results was reversed when the goal was to identify target colour. Importantly, the behaviour of the patient mirrored this pattern, in both visual fields. Danckert et al proposed that this indicates that perceptual awareness of neglected stimuli is not a prerequisite for top down processes to influence visual selection, and thus that goal driven attentional processes in the patient can modulate information processing in the patients neglected field. Such an observation is also in keeping with the finding in the present results that the patients studied, like the controls, showed elevated capture for distracters that shared the target colour.

Following on from the work of Danckert et al (1999), Snow and Mattingley (2006) examined goal driven selection in patients with right hemisphere lesions and neglect in a similar flanker task. Subjects were presented with a central letter, which was flanked on both sides by a briefly presented irrelevant flanker letter. Both target and flanker could be congruent or incongruent on either colour or letter. Subjects had to either report the letter or the colour of the target, thus the same feature of the flanker would be either congruous or incongruous on this task relevant aspect. With regard to the task relevant feature of the flanker, latencies to identify the target were slowed when the relevant feature of the flanker was incongruent, on both sides. Snow and Mattingley argued that this indicates that for both visual fields, the patients can prioritise features relevant for performance and thus that goal driven selection is intact for contralesional stimuli. These findings are also in keeping with the finding in the present results that the patient groups, like the controls, showed elevated capture for distracters that shared the target colour.

With regard to the other, irrelevant feature of the flanker (i.e. colour feature if the task was to identify the target letter), a differential pattern was revealed for the patient group, namely that, whilst there were no observed effects for left sided flankers, for right sided flankers latencies to identify the target were slowed when the flanker was incongruent with regard to this feature. Snow and Mattingley take this as evidence for a breakdown in the selective processing of visual features on this 'intact' side. They argue that this indicates that the patients studied have impairment in the inhibition of irrelevant information in their intact field. Thus, that brain areas involved in the coding of visual salience received ineffective goal driven signals to search for a particular feature. Thus, a salience imbalance between stimulus and goal driven signals occurs in the patients, which could result in the overwhelming of goal driven signals on the ipsilesional side. Snow and Mattingley also point to the findings of Peers et al (2005), which indicated that both frontal and parietal areas may be involved in goal driven selection.

Although the Snow and Mattingley (2006) study differed much in its design from the present study, the results of the present study indicated a pattern of results that differed from the ipsilateral distractibility described by Snow and Mattingley with regard to the irrelevant feature of the flanker. When the present results were examined in terms of spatial modulation, both cortical and sub-cortical patients demonstrated a pattern of results that indicated greater distractibility when the target was on the left side of the screen. However, I observed no significant group by target side by distracter side interaction, but the pattern of the group means particularly with regard to the cortical group suggests an extinction like effect when the target was on the right and the additional distracter on the left. Although this pattern is also demonstrated by the other two groups to a lesser degree as indicated by the

significant target side by distracter side interaction, the means of the cortical group of patients appear to indicate that they are somewhat more distracted in this case when the distracter is on the right compared to the left side. Although also explainable as an extinction effect, this is in keeping with the elevated distractibility for ipilesional flankers demonstrated by Snow and Mattingley with their different design.

The present results indicated that the patient groups were more strongly distracted by similar distracters when they appeared with a sudden onset, providing evidence for computation of both goal and stimulus driven salience taking place in the patient groups. Additionally, the patient group provided evidence that they were additionally distracted, relative to controls, by distracters that appeared with a sudden onset, relative to those that appeared without a sudden onset. Individual confidence analysis indicated that increased distractibility was also demonstrated by patients whose lesions spared the frontal lobe. To further examine disturbances in the computation of salience in this group of patients in a far simpler experimental design, where again subjects have to both inhibit a response and generate a goal driven saccade, the patients were next asked to undertake an anti-saccade task. It is anticipated that the same disruptions that occurred in the present study, in terms of increased distractibility, should also be demonstrated in an anti-saccade task.

Chapter 4

Introduction

The findings reported in chapter 3 indicated that both cortical and subcortical groups of patients were more strongly distracted by similar distracters when they appeared with a sudden onset. Additionally, the patient groups provided evidence that they were additionally distracted by stimuli that appeared with a sudden onset, and that this increased distractibility was also demonstrated by patients whose lesions spared the frontal lobe. In order to further test the ability of patients with right hemisphere lesions to inhibit a response and generate a goal driven saccade, the patients were asked to return to the laboratory to take part in a further series of three eye movement tests that measured their ability, relative to healthy controls, to generate stimulus driven saccades in a prosaccade task, inhibit saccades in a fixation task, and thirdly to simultaneously inhibit stimulus driven saccades and instead generate volitional saccades in a different direction.

The antisaccade task of Hallet (1978) is ideal for the latter condition. Whilst the task appears simple (a participant who is centrally fixating a screen is presented with a peripheral stimulus and is required to make a saccade away from the stimulus), it involves several distinct processes. Relative to a situation where a participant is required to make a prosaccade towards the stimulus, the antisaccade condition requires the individual to covertly orient attention toward the stimulus, suppress an eye movement towards it and instead remap the stimulus coordinates to the new location in the opposite side of the screen (Connolly, Goodale, Desouza, Menon and Vilis, 2000). See Everling and Fischer (1998), Munoz and Everling (2004), and Hutton and

Ettinger (2006) for reviews related to basic properties, cellular activity and psychopathology respectively.

Some basic properties of the antisaccade task

It has been observed that, compared to a prosaccade task were an individual is requested to make a saccade to a suddenly appearing peripheral stimulus, the antisaccade task generates more errors, in that the participant more often moves their eyes in the wrong direction (Forbes and Klein, 1996). Interestingly, Mokler and Fischer (1999) have reported that during an antisaccade task where participants were required to indicate for each trial whether or not they made an erroneous prosaccade, that on average half of all errors were not detected by the participant, and that mean latencies for correction times between perceived and unperceived errors were significantly different from each other, with unrecognised corrections faster.

Some basic manipulations that can modulate saccadic latencies or error rates in the task include the eccentricity of the stimulus and the timing of the offset of the fixation circle at peripheral stimulus onset. Fischer and Weber (1997) reported some evidence in a subset of their sample that saccadic latencies of correct antisaccades were affected by the eccentricity of the stimulus, with increasing eccentricity resulting in a decrease in latency and an increase in errors.

A more common manipulation is to remove the central fixation circle prior to stimulus onset. A fixation offset effect is often reported, in that saccadic latencies are reduced relative to those obtained when central fixation remains on. Forbes and Klein (1996) examined the effect of temporally varying the offset of the central fixation stimulus in both pro and antisaccade tasks. They reported that for both types of task that latencies were lower in the

200msec offset condition than in the 0 msec condition, which was in turn lower than in the no offset condition. Related to this Fischer and Weber (1997) reported that the most effective gap duration between fixation offset and stimulus onset for reducing saccadic reaction time was around 200 msec. The saccadic latency change observed with prior fixation offset is attributed to the release of fixation activity in the superior colliculus (Munoz and Everling, 2004). However, in addition to influencing latencies, this manipulation can also affect accuracy. Forbes and Klein reported that more errors were made in the 200msec condition, with errors particularly marked in the antisaccade 200 msec offset condition whilst latency differences resulting from a fixation offset effect were smaller with antisaccades compared to prosaccades.

Latency

Given that additional steps are required for successful antisaccade performance, it is perhaps unsurprising that it is commonly reported that latencies to initiate prosaccades are lower than latencies to initiate antisaccades (O'Driscoll et al, 1995; Forbes and Klein, 1996; Everling, Krappmann and Flohr, 1997; Kimmig et al, 2001; Ettinger et al, 2005). Indeed, Fischer, Biscaldi and Gezeck (1997) reported that subjects who made a large number of very fast 'express' saccades in a prosaccade task also generated a high degree of errors in an antisaccade task.

Antisaccades and brain injury

The antisaccade task is extremely sensitive to brain injury. In their review Everling and Fischer (1998) observe that differential performance in the task has been reported with brain lesioned individuals, and individuals with pathologies including Alzheimer's disease, Parkinsons disease, Huntingdon's

disease, obsessive compulsive disorders and schizophrenia. Heitger et al (2004) have in fact reported acute deficits in the task in patients with very mild head injury. In the psychiatric literature, McDowell et al (2002) compared the performance of patients with schizophrenia and healthy controls in the task. Higher error rates for schizophrenics were reported, and, in contrast to healthy participants, no differences in brain activation were observed between pro- and antisaccades. Frequently a frontal lobe inhibitory deficit is viewed as being the principle source of dysfunction in the task.

Antisaccades and the frontal lobes

In their highly influential paper, Pierrot-Deseilligny, Rivaud, Gaymard and Agid (1991) examined the performance of patients with lesions to posterior parietal cortex or dorsolateral prefrontal cortex in both prosaccade and antisaccade tasks. Pierrot-Deseilligny et al reported bilateral increases in saccadic latency for prosaccades in patients with right posterior parietal cortex lesions, and less severely and only contralaterally for those with left sided lesions in this area. Conversely, patients with lesions to prefrontal cortex demonstrated a higher error rate in the antisaccade task. Pierrot-Deseilligny et al interpreted their findings as indicating that the posterior lesioned group showed a lack of excitation whilst the frontal patients showed a lack of inhibition. Therefore, they concluded that the posterior parietal cortex is involved in the triggering of reflexive saccades, whilst the prefrontal cortex is involved in the inhibition of the triggering of such saccades.

Everling, Spantekow, Krappmann and Flohr (1998) conducted electrophysiological analysis of healthy subjects participating in an antisaccade task and reported that whilst both correct antisaccades and erroneous prosaccades were both associated with a negative potential over the

dorsomedial frontal cortex, that additionally this potential was higher in the case of correct antisaccades.

However, O'Driscoll et al (1995), examining healthy adults with both tasks whilst PET scans were obtained reached a different conclusion. Whilst O'Driscoll et al reported higher levels of activation during antisaccade performance in areas including the frontal eye fields and the superior parietal lobe than those they detected whilst subjects performed prosaccades, they reported no difference in levels of activation of dorsolateral prefrontal cortex between antisaccade and prosaccade conditions. Thus O'Driscoll et al reported that higher levels of activation in these frontal areas in antisaccades are not the principal difference between performance of reflexive prosaccades and antisaccades.

Conversely, McDowell et al (2002), employing fMRI, compared activity between pro- and antisaccades and reported that the healthy controls they tested had higher levels of activity in the dorsolateral prefrontal cortex lateralised to the right hemisphere, but no differences in activity in frontal eye fields, supplementary eye fields or posterior parietal cortex were observed. Differences in prefrontal activity in healthy controls between pro- and anti-saccade tasks were interpreted by the authors as evidence that the prefrontal cortex is part of the network that must be functional for correct performance of the antisaccade task.

Additional evidence for dorsolateral prefrontal cortex activity in the antisaccade task has also been more recently provided by the imaging study of Matsuda et al (2004) and also by Ettinger et al (2005) who reported that error rates in the antisaccade task were correlated with grey matter volume in the middle frontal gyrus in the right hemisphere in healthy adults. However, the evidence to date suggests an extensive network of cortical and subcortical

structures are involved in the successful performance of the antisaccade. With regard to frontal structures, Everling et (1998) report from their review that evidence to date has implicated the frontal eye fields, supplementary eye fields, anterior cingulate cortex and dorsolateral prefrontal cortex as having higher degrees of activity when participants conduct antisaccades compared with prosaccades. Therefore whilst there is good evidence that the dorsolateral prefrontal cortex provides an inhibitory component for the antisaccade task, there is clear evidence that both other frontal structures and indeed posterior structures are involved in the successful completion of the task.

A distributed network of eye movements

Pierrot-Deseilligny, Ploner, Müri, Gaymard and Rivaud-Péchoux (2002) review evidence which points to three cortical areas which can trigger a saccadic eye movement: the frontal, supplementary and parietal eye fields, involved respectively in volitional saccades, complex eye movements, and reflexive saccades. Additional involvement of dorsolateral prefrontal cortex is required in the case of antisaccades to inhibit erroneous prosaccades, whilst the triggering of the correct antisaccade involves frontal eye field control. Indeed, Kimmig et al (2001) demonstrate the distributed network of antisaccade performance in a study employing fMRI, which contrasted prosaccade and antisaccade task performance. Kimmig et al reported that, with regard to regional activity, significantly higher activation in the antisaccade task than the prosaccade task was found in precuneus, superior parietal lobule and frontal eye field.

A recent ERP study by Mathews, Flohr and Everling (2002) clearly demonstrates the distributed network involved in their comparison of antisaccade, prosaccade and fixation blocks in healthy adults. Mathews et al

compared the signals from the three types of trials, surmising firstly that a comparison of signals between prosaccades and antisaccades would be indicative of the switch in motor set between the two types of saccades. Mathews et al further surmised that a comparison of signals between prosaccades and the maintenance of central fixation would be indicative of brain activity associated with saccadic suppressions. Finally, they proposed that a comparison of trials involving the maintenance of central fixation and those requiring an antisaccade would be indicative of the brain activity associated with the switch of motor set to an antisaccade. Comparing signals between prosaccade and antisaccade activity demonstrated modulation of frontal, frontocentral, central and parietal sites. Mathews et al postulated that the frontal activity relates to inhibition whilst central and posterior activation is more related to the preparation for a sensorimotor transformation required for the generation of antisaccades. Conversely, the inhibition of a prosaccade in the condition of maintaining central fixation brought about a modulation of frontal and frontocentral areas only. Finally, more posterior changes were associated with the comparison of antisaccades and maintaining central fixation, with modulation of central and parietal areas. This difference in activity was postulated to reflect the higher levels of preparatory activity associated with antisaccades compared to just inhibiting an eye movement. Cortically these differences were postulated to implicate the parietal and supplementary eye fields.

Indeed, whilst in general the activity of the supplementary eye fields is thought to indicate more complex saccadic behaviour, as would be found in a series of saccades (Pierrot-Deseilligny et al, 2002), this area has also been implicated in antisaccades. Schlag-Rey, Amador, Sanchez and Schlag (1997) report higher discharge rates prior to antisaccades in the supplementary eye

fields of rhesus monkeys compared to prosaccades and lower rates when prosaccades were made in error. Schlag-Rey et al propose that the supplementary eye field works in tandem with differentially contributing frontal areas including the dorsolateral prefrontal cortex and frontal eye fields for successful antisaccade performance. Activity in this area was also reported by Sweeney et al (1996) in addition to bilateral dorsosolateral prefrontal cortex, parietal cortex, right frontal eye field, putamen and left thalamus.

Other studies also highlight the distributed cortical network involved in the antisaccade task. In a PET imaged study with healthy subjects Doricchi et al (1997) reported that, relative to a prosaccade task, an antisaccade task resulted in activations of bilateral superior frontal sulcus, left frontal eye field and right supplementary eye field. Bilateral activation was also found in dorsolateral and medial frontal cortex, superior parietal lobule, inferior parietal lobule and anterior cingulate cortex. DeSouza, Menon and Everling (2003) proposed that increased activation in frontal eye fields and the dorsolateral prefrontal cortex in the antisaccade are indicative of top down suppression of saccadic activity in the superior colliculus, to prevent a reflexive prosaccade.

Therefore, whilst the dorsolateral prefrontal cortex is involved in the inhibition of the incorrect eye movement in the antisaccade task, other evidence suggest that central and posterior cortical activity is also detectable during the task. Such posterior involvement may be related to the sensorimotor transformation required for the antisaccade. Additionally, a possible contribution from the supplementary eye fields has been reported.

Cortical areas involved in eye movements: The frontal eye fields

The frontal eye fields, located close to the hand and face areas of the motor cortex (Rafal, 2006) are frequently implicated in the performance, successful or otherwise, of the antisaccade task. Examining changes in brain activity in the frontal eye field, Sweeney et al (1996) reported a progressive increase in activation from a simple fixation condition to reflexive saccades to volitional saccades, and that this region is involved in both reflexive and volitional eye movements. Connolly, Goodale, Desouza, Menon and Vilis (2000) reported, with fMRI, a significant increase in FEF activity for antisaccades compared to prosaccades. Connolly et al interpreted their findings as indicative that the human frontal eye field codes both the intention and readiness to perform a particular type of eye movement.

In an earlier study, Burman and Bruce (1997), in primate single cell stimulation studies, provided evidence that the primate frontal eye field is involved in the suppression of voluntary saccades. A delay in the initiation of task related saccades was observed following electrical stimulation of some frontal eye field cells. Burman and Bruce speculated that suppression streams from the frontal eye fields and through the colliculus and thus that saccadic inhibitory dysfunction, as demonstrated by patients with frontal lesions is connected to the loss of frontal eye field suppressive capability.

Employing transcranial magnetic stimulation (TMS), Olk, Chang, Kingstone and Ro (2006) devised a paradigm whereby both prosaccades and antisaccades required inhibition, through the use of a peripheral direction indicating chevron. Olk et al applied TMS to the right frontal eye field and reported an effect of TMS on the latencies of rightward antisaccades only. Olk et al interpreted their finding as indicative of impairment in inhibition processes of the frontal eye field, whereby the frontal eye field is involved in

the inhibition of reflexive contralateral saccades. Olk et al proposed, however, that inhibition may not play equivalent roles in saccades to or away from stimuli.

Other studies have implicated a possible cingulate eye field. Gaymard et al (1998a) reported impairments, relative to controls, on the performance of two patients with lesions to anterior cingulate cortex in several eye movement tasks. Gaymard et al hypothesised that a possible function of the anterior cingulate cortex is to enhance the occurrence of eye movements through early activation of the frontal and supplementary eye fields and the dorsolateral prefrontal cortex. Related to this, Milea et al (2003) proposed that the posterior anterior cingulate cortex is involved in the suppression of unwanted visually guided saccades, likely through connections to the prefrontal cortex.

Antisaccades and the parietal lobes

However, as previously indicated, the antisaccade task is far from being the sole province of the frontal lobe. Several researchers have implicated the involvement of inferior and superior parietal areas, and the intraparietal sulcus in the completion of the task. In a recent review, Rafal (2006) points out that both the frontal and parietal lobes have oculomotor regions, the frontal and parietal regions, at the junction of the superior frontal sulcus and precentral sulcus and in the intraparietal sulcus respectively, which are connected to each other and both also to the colliculus. Lesions to the FEF can cause persistent impairment in generating voluntary contralesional saccades and stimulus driven ipsilesional saccades. Rafal (2006) proposes that with regard to oculomotor cortex, frontal cortex is vital for the generation of voluntary saccades and parietal cortex is vital for providing the required sensorimotor transformations.

Matsuda et al (2004) reported parietal lobe involvement in their fMRI prosaccade-antisaccade comparison. Comparing the two types of tasks, Matsuda et al reported that bilateral frontal eye fields, parietal eye fields, inferior parietal lobules, anterior cingulate cortex, thalamus, and dorsolateral prefrontal cortex were more active for the antisaccade task. Connolly, Goodale, Desouza, Menon and Vilis (2000) reported that a region in posterior superior parietal cortex was more active in an antisaccade compared to a prosaccade task whilst another area, the middle inferior parietal region was active only in the antisaccade task in an fMRI study. DeSouza et al (2003) also reported, in an interleaved block of prosaccades and antisaccades that during the instructional fixation period that there was some evidence for the intraparietal sulcus regions to show higher activity for antisaccade preparation.

I referred earlier to the common finding that a successful antisaccade requires more time to initiate than a successful prosaccade. Related to this, Evdokimidis, Constantinidis, Liakopoulos and Papageorgiou (1996) manipulated, in healthy subjects, prior knowledge of the saccade type required and stimulus location in antisaccade and prosaccade tasks and reported that latencies for antisaccades were higher than those for prosaccades only in conditions were the target location was unpredictable. They argued that posterior parietal areas are involved in converting a sensory signal into a motor plan: when both manipulated factors were unpredictable, parietal areas would first create a motor plan based on the location of the stimulus, which is transferred to frontal areas which then either inhibit or release a pro stimulus saccade. If the saccade is inhibited, the posterior parietal cortex then in turn creates a new motor plan to the other side of the screen. Therefore, inter lobe communication explains latency differences between the two types of task.

With regard to heightened activation in the parietal cortex, Sweeney et al (1996) reported that bilateral parietal activation was seen in both their standard and conditional antisaccade tasks in the superior and inferior parietal lobules, which may be related to the internal mapping of sensory representations. Related to this, Doricchi et al (1997), with regard to the inferior parietal lobule activation observed in their antisaccade task, proposed that this was related to sensory-motor activation related both to attentional disengagement from the initial cue and the recomputation of the new saccadic vector for the antisaccade on the basis of the cue. Similarly, Everling, Spantekow, Krappmann and Flohr (1998) reported from their ERP study that the performance of an antisaccade was preceded by the shift of negative potential from the parietal hemisphere opposite to the stimulus, to the parietal hemisphere on the same side as the stimulus. This was interpreted as being neural evidence of the change of a motor plan during the programming of antisaccades.

Terao et al (1998), applying transcranial magnetic stimulation (TMS) whilst subjects took part in an antisaccade task, reported that onset latency of antisaccades was most affected at 80 msec after target presentation over posterior parietal regions, whilst the most marked delay in onset at 100msec after target presentation was over frontal regions. Terao et al described their frontal region as including the frontal eye field, whilst the posterior region included the posterior parietal cortex. They propose a model of cortical activity during antisaccadic task performance where a visual signal from the right hemifield arrives at left primary visual cortex, is then passed to left parietal cortex, which passes the information to the opposite parietal cortex. Then the bilateral information is transferred to the frontal cortex including the frontal eye field. Finally, the signal in the left frontal eye field is passed to the

right frontal eye field and from there the final motor output is sent to generate a saccade to the left.

Based on their findings in patients with dorsolateral prefrontal lesions sparing the eye fields, Pierrot-Deseilligny et al (2003) argue that uninhibited parietal eye fields generate error saccades in the antisaccade task, whilst inhibition comes not from the frontal eye field, but from the dorsolateral prefrontal cortex. However, the triggering of correct antisaccades is not controlled by the dorsolateral prefrontal cortex but rather by the frontal eye field.

Selective right hemisphere involvement

Although there is considerable evidence that the antisaccade task involves a large distributed network of cortical and subcortical areas, there is also some evidence that the task invokes some degree of right hemispheric preferential involvement. Such a bias may be in part related to the inhibitory aspect of the antisaccade task. I have demonstrated in the previous chapter that individuals with right hemispheric lesions display inhibitory impairments, and it has been demonstrated that the right hemisphere is more dominant in some forms of inhibitory tasks. With regard to lesion studies, Walker, Husain, Hodgson, Harrison and Kennard (1998) reported on a patient with a right frontal lobe infarct who had a profound bilateral deficit in an antisaccade task.

With regard to inhibitory function in healthy subjects, Garavan, Ross and Stein (1999), employed fMRI in a simple task involving a stream of single letters, with subjects instructed to respond to one of a pair of alternating targets and inhibit a response to the other. A predominantly right lateralised distributed network of brain areas were identified as being associated specifically with the inhibitory response, including middle and inferior frontal

gyri, the inferior parietal lobe, angular gyrus and insula. In the antisaccade task, McDowell et al (2002) reported higher levels of activity in the dorsolateral prefrontal cortex lateralised to the right hemisphere, when comparing brain activity between pro- and antisaccadic tasks, and additionally DeSouza, Menon and Everling (2003) have reported right dorsolateral prefrontal cortex involvement in both antisaccades and prosaccades relative to fixation.

Indeed Ford, Goltz, Brown and Everling (2005) comment on antisaccade related right hemispheric lateralisation related to correct performance in their event related fMRI study. They employed interleaved prosaccade and antisaccade trials and a long preparatory, trial-indicative fixation period to examine cortical activity related to preparation. The analysis indicated that during the later proportion of the preparatory period, higher activation for correct antisaccade trials compared to correct prosaccade trials was observed in an extended network of frontal and parietal areas. When comparing correct and incorrect antisaccade trials in this same preparatory period, correct antisaccades were related only to higher activations in frontal lobe areas including right dorsolateral prefrontal and anterior cingulate cortex. Ford et al proposed that frontal cortical activation prior to stimulus onset is associated with performance levels in the antisaccade task, and that the areas with differential activity in correct trials may be involved in saccadic suppression.

Posterior lesions and antisaccades

Although to date there is little doubt that lesions to the frontal lobe result in deficits in the antisaccade task, there is less conclusive evidence about dysfunction in the task following lesions to the parietal lobe. Pierrot-Deseilligny et al (1991) reported no dysfunction in the task and instead reported bilateral increases in saccadic latency for prosaccades in patients

with right posterior parietal cortex lesions, particularly for patients with right sided lesions. They concluded that the posterior lesioned group showed a lack of excitation in the task.

Machado and Rafal (2004) also failed to observe a difference in error rate between a group of older adult healthy controls and a group of patients with lesions involving posterior association cortex. However, Machado and Rafal reported evidence of an asymmetry in the error rates of the patient group, namely that they made more errors towards ipsilesional stimuli. Furthermore, this group of patients also generated slower antisaccades away from contralesional stimuli. At the same time Machado and Rafal (2004a) reported that in a prosaccade task that the same group of patients were able to make use of a predictive central cue in a prosaccade task and displayed no field asymmetries with regard to saccadic latencies. Rafal (2006) in fact argues that lesions to parietal oculomotor cortex do not relate to deficits in stimulus driven saccadic programming and thus that deficits such as increased latencies for contralateral saccades are more related to attentional deficits. Therefore the evidence would appear to suggest that posterior lesions should not result in increased distractibility in the antisaccade task.

Experiment 7: Inhibitory deficits in patients with right hemisphere subcortical and posterior cortical lesions in an antisaccade task

The results of experiment 6 indicated that the patient groups were more distractible than the older adult control group. Evidence was also provided that such increased distractibility was also demonstrated by patients whose lesions spared the frontal lobe. To further examine disturbances in the ability of the patients to inhibit a response and generate a goal driven saccade the patients were asked to participate in a further eye movement study were in one block they would be required to generate antisaccades, in a further block generate prosaccades and in a third block demonstrate complete saccadic inhibition through maintaining central fixation.

Method

Healthy Participants

A new group of twelve elderly control subjects (4 male, 8 female; mean age 73.2, SD 5.1) took part in the experiment and were reimbursed for travel expenses.

Patients

The same 6 patients with sub-cortical lesions (mean age at testing, 63.0, SD 10.1) and the same 7 patients with cortical lesions (mean age at testing 65.6, SD 9.9) were included in the study, lesion chronicity for cortical and sub-cortical patients at the time of testing can be seen in table 7.1. The study was conducted in accordance with the ethical guidelines of the South

Glasgow University Hospitals NHS trust and the Declaration of Helsinki. All participants gave their informed consent prior to the study.

Table 7.1: Lesion chronicity of patients participating in Antisaccade study[1].

Cortical group	Patient	Chronicity at test (months)
	TH	31
	JC	3
	JHH	4
	JS	6
	JM	38
	HM	33
	JB	23
Subcortical group	**Patient**	
	GM	44
	MK	31
	LM	30
	JQ	3
	AA	17
	BM	4

Apparatus and stimuli

Example displays are shown in figure 7.1. A centrally presented white circle with a diameter of 0.6° on a black background served as a fixation circle. Stimuli consisted of a single square white stimulus, 0.6° in size, which would appear peripherally in each trial at one of two possible locations on the horizontal meridian, either 7.3° to the left or right of the centre of the screen (the same location as the additional distracter in the preceding study).

Displays were presented and responses recorded using the same equipment employed in the preceding study. Correct antisaccades/prosaccade trials were defined as trials were, following stimulus onset, the first saccade was made at least one degree into the hemifield contralateral/lateral to the

[1] In all tables in this chapter, patients who had a BIT score indicative of neglect are indicated in italics

stimulus. Trials on which the central disk was not properly fixated (deviation larger than 1°) at presentation of the search display were excluded from analysis. Trials on which observers made a saccade with latency shorter than 80 ms were considered anticipatory and were excluded from further analysis (after Machado and Rafal, 2000). Moreover, trials with no, or too small (shorter than 1°) a saccade were rejected.

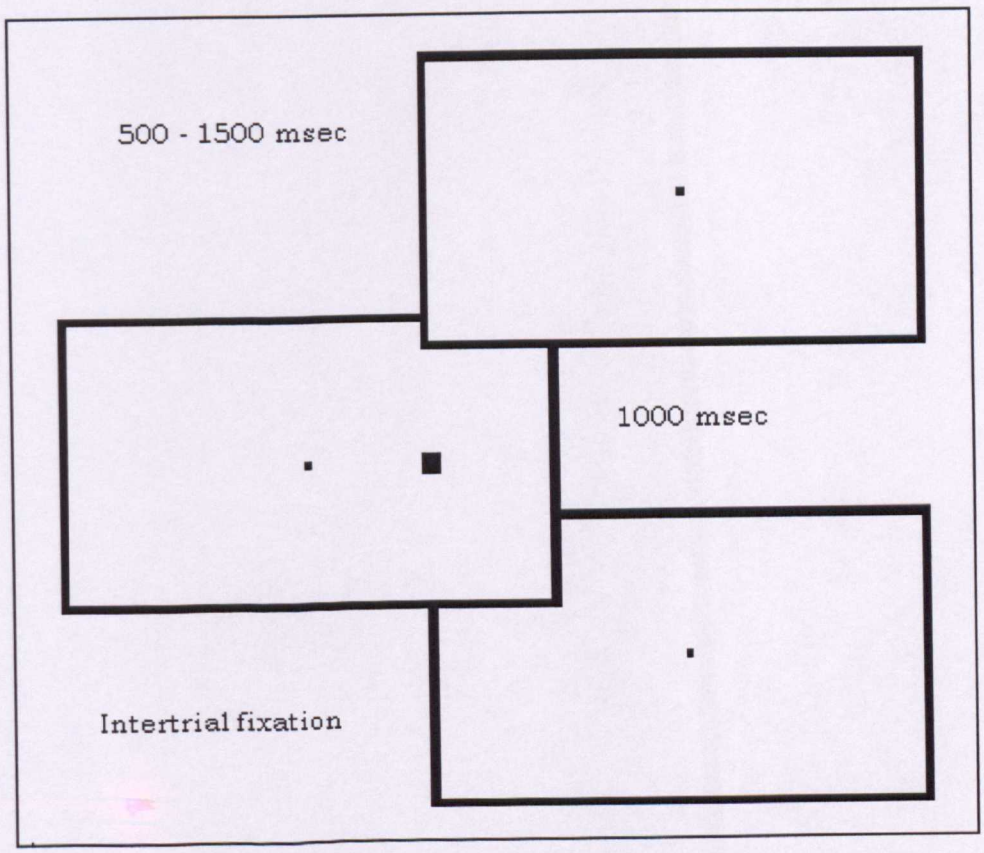


Figure 7.1: Stimulus display in antisaccade, prosaccade and fixation condition

Employing these criteria in the antisaccade condition resulted in 23.9% of the patients, and 8.9% of the control group's trials being rejected. A further 1% of the control group's and 1.3% of the patients trials were rejected due to recording errors or a failure to saccade. Employing these criteria in the prosaccade condition resulted in 26.4% of the patients, and 10.2% of the control group's trials being rejected. A further 0.1% of the control group's and

1.7% of the patients trials were rejected due to recording errors or a failure to saccade.

In the fixation condition, a correct trial was defined as one where, for the duration of the trial, the participant was able to maintain fixation within 1° of the central fixation circle. Trials were the central disc was not properly fixated (deviation larger than 1°) at presentation of the search display were excluded. This criterion resulted in 7.8% of the control group and 5.9% of the patients data being rejected. A further 0.2% of the control and 0.1% of the patients data were rejected due to recording errors.

Procedure

Calibration procedures were carried out employing the method used in the preceding study. In all conditions subjects were instructed to begin each trial by fixating on the central circle on the screen. In the antisaccade condition, participants were instructed to maintain central fixation until they detected a single white box appear peripherally on the screen, and then look to the same place on the opposite side of the screen away from the white box as quickly as possible, without looking at the stimulus. In the prosaccade condition participants were instead instructed to make a saccade towards the white box as quickly as possible. Finally, in the fixation task participants were instructed to ignore the peripheral stimulus in each trial and instead maintain central fixation throughout the block.

Prior to each block participants were shown a 10 trial demonstration of the task to illustrate the instructions. Each block consisted of 40 leftward and 40 rightward peripheral stimuli trials, randomly intermixed. The order of blocks was counterbalanced between subjects. Patient JQ kindly agreed to

undertake 2 blocks of each condition and patient GM an additional antisaccade block.

In between trials a fixation display was presented, consisting of just the central fixation disk. When properly fixated by the observer, the experimenter initiated a new trial and, if necessary, an automatic spatial drift correction was performed. An experimental trial consisted of the continued presence of the central fixation circle for a random duration of 500 to 1500 msec (to reduce anticipatory responses), followed by the onset of the stimulus to one side of the screen (thus the central fixation circle remained on the screen throughout the trial). The stimulus remained on the screen for 1000 msec, the offset of which signified the end of the trial.

Results

Fixation condition

For each participant in the fixation task, the mean percentages of trials were the participant was able to maintain central fixation was calculated.

Table 7.2: Means per subject for fixation task for control, cortical and subcortical groups. Asterisks indicate outwith confidence interval of control group.

Group		Mean accuracy
Control		92.7% (99% CI: 87.12%-98.3%)
Cortical	*TH*	85.9%*
	JC	92.4%
	JHH	61.3%*
	JS	1.3%*
	JM	47.5%*
	HM	48.0%*
	JB	86.3%*
Subcortical	GM	88.5%
	MK	66.2%*
	LM	79.7%*
	JQ	85.5%*
	AA	98.7%
	BM	94.9%

As in the previous chapter, the patient results were arranged into cortical and subcortical groups for subsequent analysis. Across control, cortical and subcortical groups, the mean percentage of trials in which participants were able to maintain central fixation was 93%, 60% and 86% respectively. Per subject means can be seen in table 7.2, along with 99% confidence interval based on the performance of the control group. Patients whose performance was outside the control confidence interval are indicated with asterisks.

Group differences in ability to perform the task were examined by means of one-way ANOVA (the data was found to violate the assumption of homogeneity, however Arcsin transformation, which removed this violation revealed the same significant group differences and therefore transformed ANOVA data is reported), and planned comparisons with Bonferroni tests. One way ANOVA revealed a significant effect of Group, $F(2,22)=7.99$, $p<.01$. Planned comparisons revealed a significant difference between the control group and the cortical group ($p<.01$) and a trend to a difference between the cortical and subcortical groups ($p=.08$). Thus the analysis indicates that the control group performs significantly better than the cortical group, but not the subcortical group, who do not differ from the control group.

Prosaccade condition

For each participant in the prosaccade condition, the mean percentage of trials were the subject successfully initiated a saccade towards the stimulus was calculated. Across control, cortical and subcortical groups, the mean percentage of trials in which participants were able successfully perform a prosaccade was 100%, 99% and 99% respectively. Per subject means for patient groups can be seen in table 7.3.

Table 7.3: Means per subject for prosaccade task for control, cortical and subcortical groups.

Group		Mean accuracy
Control		100.0%
Cortical	*TH*	100.0%
	JC	100.0%
	JHH	100.0%
	JS	98.2%
	JM	96.0%
	HM	100.0%
	JB	100.0%
Subcortical	GM	97.0%
	MK	100.0%
	LM	100.0%
	JQ	97.8%
	AA	100.0%
	BM	98.5%

Clearly the participants found the prosaccade condition unproblematic. The next analysis conducted on the data from the prosaccade condition was in terms of overall saccadic latencies. Mean saccadic reaction times (SRT) for control, cortical and subcortical groups in the prosaccade task were 219msec, 199msec and 227msec respectively. Per subject means for patient groups can be seen in table 7.4.

Table 7.4: Mean SRT for correct prosaccades for control, cortical and subcortical groups

Group		Mean
Control		219 msec
Cortical	*TH*	252 msec
	JC	301 msec
	JHH	144 msec
	JS	177 msec
	JM	190 msec
	HM	148 msec
	JB	181 msec
Subcortical	GM	176 msec
	MK	211 msec
	LM	273 msec
	JQ	243 msec
	AA	249 msec
	BM	208 msec

Group differences in saccadic latency to perform the prosaccade task were examined by means of one way ANOVA, which indicated no significant differences in latency between Groups ($F(2,22)=.45$, $p>.05$).

Latencies were next examined with regard to any possible spatial modulation with regard to leftward or rightward targets in the prosaccade condition. Mean SRT for controls and patients for leftward and rightward correct prosaccades can be seen in table 7.5. In order to examine possible group differences in saccadic latencies to leftward and rightward stimuli in more detail a two way mixed ANOVA with within subjects factor of Stimulus Side and between subjects factor of Group (control, cortical and subcortical) was conducted. However this analysis indicated no significant effect of either Stimulus Side or Group ($F(1,22)=2.96$, $p>.5$ and $F(2,22)=.50$, $p>.6$, respectively).

Table 7.5: Mean correct SRT in milliseconds for control group and patients by stimulus side for prosaccade condition

Left stimulus		Mean SRT	Right stimulus		Mean SRT
Control	**Mean**	**214**	**Control**	**Mean**	**223**
Cortical	*TH*	254	**Cortical**	*TH*	250
	JC	299		*JC*	302
	JHH	114		JHH	164
	JS	245		*JS*	115
	JM	274		*JM*	130
	HM	142		HM	153
	JB	219		JB	146
	Mean	**221**		**Mean**	**180**
Subcortical	GM	177	**Subcortical**	GM	174
	MK	210		MK	213
	LM	253		LM	296
	JQ	346		*JQ*	171
	AA	279		AA	219
	BM	204		BM	213
	Mean	**245**		**Mean**	**214**

The final analyses of the prosaccade condition focussed on saccadic amplitudes. Mean saccadic amplitude in degrees for control, cortical and subcortical groups were 8.5°, 7.8° and 7.5° respectively. Group means and per subject means for patient groups can be seen in table 7.6.

Table 7.6: mean saccadic amplitude in degrees for correct prosaccades by group

Control	**mean**	8.5°			
Cortical	*TH*	8.8°	**Subcortical**	GM	7.4°
	JC	5.7°		MK	7.2°
	JHH	9.4°		LM	7.6°
	JS	8.6°		*JQ*	6.5°
	JM	6.0°		AA	8.2°
	HM	8.1°		BM	8.1°
	JB	7.7°		**mean**	7.5°
	mean	7.8°			

The table above appears to suggest that on the whole, both patient groups make smaller amplitude saccades than the control group. However, the measurements of saccadic amplitude for the three groups violated the assumption of homogeneity of variance, and this was not correctable with either logarithmic or root transformation. Therefore to examine group differences, a Kruskal-Wallace test was conducted, which revealed only a trend to amplitude differences between the groups ($\chi^2(2)=5.47$, $p=0.65$). In order to examine saccadic amplitude in more detail, mean amplitudes were obtained for correct prosaccades to leftward and rightward stimuli. Control and patient means can be seen in table 7.7.

Table 7.7: Control and patient mean saccadic amplitudes for correct leftward and rightward prosaccades.

Left stimulus			**Right stimulus**		
		Amplitude			**Amplitude**
Controls	**mean**	8.6°	**Controls**	**mean**	8.3°
Cortical	*TH*	9.3°	**Cortical**	*TH*	8.3°
	JC	4.6°		*JC*	6.9°
	JHH	8.0°		JHH	10.4°
	JS	10.2°		*JS*	7.1°
	JM	3.8°		*JM*	7.5°
	HM	7.7°		HM	8.6°
	JB	7.2°		JB	8.1°
	Mean	7.2°		**Mean**	8.1°
Subcortical	GM	7.7°	**Subcortical**	GM	7.2°
	MK	6.7°		MK	7.7°
	LM	7.5°		LM	7.8°
	JQ	4.2°		*JQ*	8.1°
	AA	8.5°		AA	7.9°
	BM	7.2°		BM	9.0°
	Mean	7.0°		**Mean**	7.9°

In order to examine possible group differences in saccadic amplitudes to leftward and rightward stimuli in more detail further Kruskal-Wallace tests were conducted on saccadic amplitudes for leftward and rightward

prosaccades. Significant group differences were observed for leftward saccades only ($\chi^2(2)=6.59$, $p<.05$). Follow up Mann-Whitney tests indicated a significant difference between control and subcortical groups only ($p<.01$).

Antisaccade condition

The principal measure of performance in the antisaccade condition is the error rate, which is the mean proportion of erroneous prosaccades made in the block. The per subject percentage of errors in the antisaccade condition was therefore calculated, indicating a mean error rate for controls, cortical patients and subcortical patients of 13%, 57% and 39% respectively. Per subject error rates for patients can be seen in table 7.8, along with the 99% confidence interval of the controls group's errors, with asterisks indicating which patients lie outside this interval with regard to error rate.

Table 7.8: Overall group percentage error rate for antisaccades. Asterisks indicate outwith confidence interval of control group.

Group		Percent error rate
Control		**Mean 12.7% (99% CI: 4.96% to 20.51%)**
Cortical	*TH*	16.7%
	JC	20.8%*
	JHH	62.7%*
	JS	76.8%*
	JM	90.3%*
	HM	72.9%*
	JB	57.4%*
		Mean 56.8%
Subcortical	GM	50.4%*
	MK	40.3%*
	LM	22.7%*
	JQ	89.7%*
	AA	6.3%
	BM	22.6%*
		Mean 38.7%

Group differences in mean error rate in the antisaccade condition were examined by means of one way ANOVA and planned comparisons with Bonferroni tests (again, the data were observed to violate the assumption of homogeneity, however Arcsin transformation removed the violation and transformed data is reported). ANOVA revealed a significant effect of Group ($F(2,22)=10.15$, $p<.01$), and subsequent planned comparisons indicated a significant difference in mean error rate between the control group and cortical group of patients only ($p<.01$), with a strong trend to an error rate difference between controls and the subcortical group of patients ($p=.055$). In order to examine error rates in the antisaccade condition in more detail, the per-subject errors were broken down into rates for leftward and rightward stimuli. Mean error rates for controls and individual patient rates for leftward and rightward stimuli can be seen in table 7.9.

Table 7.9: Mean percentage error rate in antisaccade condition by group and stimulus side. Asterisks indicate outwith confidence interval of control group.

Group		Left stimulus error percentage	Right stimulus error percentage
Control	**Mean**	**11.88% (99% CI: 2.34% to 21.42%)**	**14.15% (99% CI: 2.77% to 25.52%)**
Cortical	*TH*	20.59%	13.16%
	JC	38.10%*	9.38%
	JHH	100.00%*	40.54%*
	JS	71.43%*	82.35%*
	JM	85.71%*	94.12%*
	HM	83.87%*	60.71%*
	JB	65.52%*	50.00%*
	Mean	**66.46%**	**50.04%**
Subcortical	GM	41.67%*	58.21%*
	MK	58.62%*	24.24%
	LM	17.65%	28.13%*
	JQ	93.62%*	86.00%*
	AA	0.00%	12.50%
	BM	27.27%*	17.24%
	Mean	**39.80%**	**37.72%**

Again, 99% confidence intervals of the control group's performance were calculated to examine individual patient differences, which show that the vast majority of patients demonstrate a significantly higher error rate for both leftward and rightward stimuli relative to controls.

Group mean error rates in the antisaccade task were further examined by means of a mixed ANOVA with within subject factor of Group and between subject factor of Stimulus Side. Again this analysis was found to contradict the assumption of homogeneity of variance, and Arcsin transformations were conducted prior to ANOVA. ANOVA revealed no significant effect of Stimulus Side ($F(1,22)=.95$, $p>.3$), and no interaction between Stimulus Side or Group was found ($F(2,22)=1.75$, $p>.1$). However, a significant effect of Group was revealed ($F(2,22)=10.80$, $p<.01$), and pairwise comparisons indicated a significant difference between controls and the cortical patient group ($p<.001$). Furthermore, a trend to significance was again revealed between the control group and the subcortical group of patients ($p=.07$). No other comparisons indicated any significant difference, thus no difference was indicated in the analysis between the cortical and subcortical group of patients.

Relevant to an examination of error rates for patients in the antisaccade condition is the question of whether or not corrective saccades were made following an erroneous prosaccade. Successful corrections following an error indicate both that the subject understood the task and also provides some indication that they were not performing poorly due to low motivation. In order to examine this issue, for each trial in the antisaccade condition where a subject made an erroneous prosaccade, the saccade following the erroneous prosaccade was examined. This follow-on saccade was considered as a corrective antisaccade if this saccade ended on the side of the display opposite the stimulus. For controls, out of 109 erroneous prosaccades, 91 were

subsequently corrected. Total corrections and percentages for all patients can be seen in table 7.10.

Table 7.10: Percentage of trials in antisaccade condition with corrected saccades following erroneous prosaccades

Group		Total errors	Corrected errors	Percent corrected
Controls		109	91	83%
Cortical	*TH*	12	12	100%
	JC	11	6	55%
	JHH	37	33	89%
	JS	53	24	45%
	JM	28	11	39%
	HM	43	30	70%
	JB	35	22	63%
Subcortical	GM	64	47	73%
	MK	25	22	88%
	LM	15	10	67%
	JQ	87	71	82%
	AA	5	4	80%
	BM	14	13	93%

The table above demonstrates that the majority of patients clearly corrected the majority of their errors with a corrective antisaccade following their erroneous prosaccade. The two patients with the lowest rates of corrective antisaccades were both patients with cortical lesions and high overall error rates.

Following on from this, an examination was next conducted on SRT's for corrective saccades. Mean latencies for each patient for corrective saccades can be seen in table 7.11, with latencies for correct antisaccades from the same condition and correct prosaccades from the prosaccade condition provided alongside for comparison.

Table 7.11: Mean SRT for corrective antisaccades compared to correct antisaccades and correct prosaccades

Group		Corrective antisaccades*		Correct antisaccades		Correct prosaccades	
		Mean	N	Mean	N	Mean	N
Cortical	*TH*	93	(12)	316	(60)	252	70
	JC	262	(6)	596	(42)	301	42
	JHH	157	(33)	304	(22)	144	53
	JS	282	(24)	394	(16)	177	55
	JM	226	(11)	211	(3)	190	24
	HM	210	(30)	387	(16)	148	66
	JB	372	(22)	543	(26)	181	68
Subcortical	GM	165	(47)	397	(63)	176	65
	MK	143	(22)	506	(37)	211	68
	LM	132	(10)	352	(51)	273	54
	JQ	247	(71)	288	(10)	243	90
	AA	108	(4)	379	(75)	249	79
	BM	172	(13)	320	(48)	208	64

* following erronious prosaccades

It can be seen that there is a striking difference in latencies between correct antisaccade SRT's and corrective antisaccade SRT's. However, it can be seen that many patients have a small number of either corrective antisaccades or correct antisaccades (patients JC, JM and AA in particular) resulting in difficulty in obtaining reliable measures of central tendency in these patients. Therefore these means are provided purely for illustration, but provide some evidence that corrective antisaccades following erroneous prosaccades in the antisaccade condition are produced more quickly than initially correct antisaccades.

To examine correct antisaccadic latencies in some more detail, means were obtained for both correct antisaccades and errors (erroneous prosaccades). Means for each participant for both correct and incorrect responses were calculated and can be seen in table 7.12.

Table 7.12: mean SRT in milliseconds for correct and incorrect (erroneous prosaccade) trials by group in antisaccade condition

Group	Incorrect trials			Correct trials		
	Subject	Mean	N	Subject	Mean	N
Control	Mean	211msec	(109)	Mean	356 msec	(756)
Cortical						
	TH	251 msec	(12)	*TH*	316 msec	(60)
	JC	293 msec	(11)	*JC*	596 msec	(42)
	JHH	136 msec	(37)	JHH	304 msec	(22)
	JS	202 msec	(53)	*JS*	394 msec	(16)
	JM	174 msec	(28)	*JM*	211 msec	(3)
	HM	167 msec	(43)	HM	387 msec	(16)
	JB	188 msec	(35)	JB	543 msec	(26)
	Mean	201 msec		Mean	393 msec	
Subcortical	GM	175 msec	(64)	GM	397 msec	(63)
	MK	174 msec	(25)	MK	506 msec	(37)
	LM	202 msec	(15)	LM	352 msec	(51)
	JQ	250 msec	(87)	*JQ*	288 msec	(10)
	AA	307 msec	(5)	AA	379 msec	(75)
	BM	189 msec	(14)	BM	320 msec	(48)
	Mean	216 msec		Mean	374 msec	

Although it can be observed that all three groups initiate incorrect saccades (erroneous prosaccades) with a considerably lower latency than those found for correct antisaccades, it would not be possible to obtain stable measures of central tendency (particularly with regard to control errors, where 8 subjects have less than 10 errors) to conduct meaningful quantitative group analysis due to the few numbers of cells in some conditions.

A final data set related to latencies in the antisaccade task pertains to SRT for correct antisaccades away from leftward and rightward stimuli. Mean latencies for patients can be seen in table 7.13, which indicates 99% confidence intervals based on control performance and shows that the majority of patients that are outside the intervals are outside for both left and

right stimuli trials, with subcortical patient GM the exception. Again, due to the lack of observations for some patients, no group analysis was carried out.

Table 7.13: Mean SRT for patients for correct antisaccades from left and right stimuli in milliseconds. Asterisks indicate outwith confidence interval of control group.

	Left stimuli			Right stimuli		
Group	**Subject**	**Mean**	**N**	**Subject**	**Mean**	**N**
Control	Mean 359 (99% CI: 287 to 430)			Mean 352 (99% CI: 291 to 413)		
Cortical	*TH*	304	27	*TH*	325	33
	JC	655*	13	*JC*	570*	29
	JHH	~	~	JHH	304	22
	JS	397	10	*JS*	389	6
	JM	277*	2	*JM*	80*	1
	HM	350	5	HM	403	11
	JB	544*	10	JB	542*	16
Subcortical	GM	372	35	GM	429*	28
	MK	533*	12	MK	494*	25
	LM	330	28	LM	378	23
	JQ	231*	3	*JQ*	313	7
	AA	394	40	AA	362	35
	BM	311	24	BM	328	24

Finally, with regard to saccadic amplitude for correct and incorrect (erroneous prosaccade) trials in the antisaccade condition, per subject means for correct and incorrect trials are provided in tables 7.14 and 7.15. From the results below it can be seen that, like the control group, the patients in each group for both left and right stimuli appear to make smaller amplitude saccades in incorrect trials compared to correct trials. Also of theoretical interest is the question as to whether or not the patients are able to make antisaccades of similar amplitude to the controls in correct trials.

Table 7.14: Saccadic amplitude for correct trials for leftward and rightward stimuli across three groups for antisaccade condition. Asterisks indicate outwith confidence interval of control group.

	Left stimuli correct trials			Right stimuli correct trials		
Group	**Subject**	**Mean**	**N**	**Subject**	**Mean**	**N**
Control	**Mean**	**7.3°**	(392)	**Mean**	**7.7°**	(364)
	(99% CI: 5.6° to 9.0°)			(99% CI: 6.3° to 9.2°)		
Cortical	*TH*	11.4°*	(27)	*TH*	10.6°*	(33)
	JC	4.4°*	(13)	*JC*	5.1°*	(29)
				JHH	6.4°	(22)
	JS	18.9°*	(10)	*JS*	22.5°*	(6)
	JM	1.9°*	(2)	*JM*	1.0°*	(1)
	HM	6.2°	(5)	HM	4.0°*	(11)
	JB	4.9°*	(10)	JB	3.3°*	(16)
	Mean	**8.0°**		**Mean**	**7.6°**	
Subcortical	GM	3.6°*	(35)	GM	5.4°*	(28)
	MK	11.6°*	(12)	MK	10.3°*	(25)
	LM	6.9°	(28)	LM	5.6°*	(23)
	JQ	4.2°*	(3)	*JQ*	14.9°*	(7)
	AA	8.1°	(40)	AA	6.7°	(35)
	BM	11.3°*	(24)	BM	6.6°	(24)
	Mean	**7.6°**		**Mean**	**8.3°**	

Table 7.15: Saccadic amplitude for incorrect (erroneous prosaccade) trials for leftward and rightward stimuli across three groups for antisaccade condition. Asterisks indicate outwith confidence interval of control group.

	Left stimuli incorrect trials			Right stimuli incorrect trials		
Group	**Subject**	**Mean**	**N**	**Subject**	**Mean**	**N**
Control	**Mean**	**6.8°**	(51)	**Mean**	**6.8°**	(58)
Cortical	*TH*	6.6°	(7)	*TH*	6.1°	(5)
	JC	3.5°	(8)	*JC*	6.3°	(3)
	JHH	7.1°	(22)	JHH	7.3°	(15)
	JS	7.4°	(25)	*JS*	7.9°	(28)
	JM	2.6°	(12)	*JM*	7.1°	(16)
	HM	8.3°	(26)	HM	8.3°	(17)
	JB	6.9°	(19)	JB	7.7°	(16)
	Mean	**6.1°**		**Mean**	**7.2°**	
Subcortical	GM	6.0°	(25)	GM	5.2°	(39)
	MK	5.1°	(17)	MK	6.8°	(8)
	LM	5.3°	(6)	LM	5.7°	(9)
	JQ	4.9°	(44)	*JQ*	8.5°	(43)
				AA	6.6°	(5)
	BM	5.6°	(9)	BM	7.4°	(5)
	Mean	**5.4°**		**Mean**	**6.7°**	

In order to address this question in a quantifiable form, 99% confidence intervals of the controls groups saccadic amplitude for leftward and rightward stimuli in correct antisaccade trials was calculated, and patients outside these intervals are indicated on table 7.14 with an asterisk. This analysis clearly indicates, at least with regard to patients with a meaningful number of trials, that they are less accurate, both in terms of hypo- and hypermetric antisaccades compared to the control group in correct antisaccade trials.

Discussion

The results presented here focussed on the ability of cortical and subcortical right hemisphere lesioned patients to inhibit a saccade in a fixation task, generate a stimulus driven saccade in a prosaccade task, and inhibit a saccade and instead produce a volitional saccade in a different direction in an antisaccade task. In the fixation task it was demonstrated that the cortical group of patients demonstrated significant impairment in the task, whilst all participants were able to produce an accurate and timely stimulus driven prosaccade when requested. In the antisaccade task the patients (and the cortical group in particular) demonstrated significant evidence of a bilateral impairment in the task, in terms of both the accuracy of their antisaccades and their error rates in the task. The following discussion will focus in more detail on the most salient findings observed.

Healthy controls

Raemaekers, Vink, van den Heuvel, Kahn, and Ramsey (2006) compared differences in performance in antisaccades and prosaccades between young adults, mid-adulthood and old adulthood. They reported no significant group effects of age on saccadic latencies or error rates for

prosaccades or antisaccades. However, there was some correlational evidence of an effect of age on onset latencies for antisaccades but not on error rates. Everling and Fischer (1998) however observe that there is some evidence that the error rate in the antisaccade task increases with age. Olincy, Ross, Young, & Freedman (1997) previously reported age related increases in errors in the antisaccade task.

However, in the present study, the error rate of the control group in the antisaccade task was in line with the performance of a control group of older adults reported by Machado and Rafal (2004), as was their latency to perform correct antisaccades and the absence of any effect of stimulus laterality on their error rates. With regard to the prosaccade condition, Machado and Rafal (2004a) reported no hemifield asymmetry of saccadic latencies in a group of neurologically healthy adults, a finding replicated in the present study. Therefore the healthy older adult control group appeared to have performed the tasks asked of them well.

Fixation condition

In the fixation condition I measured participants ability to inhibit all saccadic responses and instead maintain central fixation whilst peripheral stimuli were flashed upon the screen. This was a useful additional measure, as Machado and Rafal (2000) have suggested that a potential source of interpretational error in antisaccade tasks is to be clear whether errors are due to problems with saccadic response inhibition or volitional saccade generation. Mathews et al (2002) reported from their ERP study that comparing prosaccade trials with maintaining central fixation would indicate brain activity indicative of saccadic suppression, and reported that such inhibition generated a modulation of frontal and frontocentral areas only.

Analysis of the ability of the patients to perform this task was measured in two ways, and both methods indicated some form of dysfunction in the patients studied. Firstly, a comparison of individual patient accuracy in the task, relative to the performance of the control group by means of confidence intervals, indicated that all but one of the cortical group of patients and half of the subcortical group of patients were impaired. Furthermore, analysis of variance indicated that relative to the control group, the cortical group demonstrated impaired performance whilst the subcortical group did not.

Therefore, whilst patients like JHH, JB, and JM, who have frontal involvement in their lesions could be expected to demonstrate inhibitory dysfunction in this task, in line with the findings of the preceding chapter we are presented with patients such as TH, JS, and HM, whose lesions spare the frontal lobe but yet these patients demonstrate significant impairment in an inhibitory task of saccadic suppression. Additionally, patients MK, LM, and JQ, whose subcortical lesions involve the thalamus and basal ganglia, also demonstrated impairment in the task. It would appear that these patients have an inhibitory deficit, or that the inhibitory capacity of their spared frontal lobes is not being properly directed.

Prosaccade condition

In the saccade condition I measured patients ability to accurately and promptly make stimulus driven saccades to a single stimulus flashed peripherally upon the screen. With regard to accuracy in the task, no patients demonstrated any notable impairment. Furthermore, analysis of overall latency to make an eye movement indicated no difference between the groups. Furthermore, no significant difference between the groups was observed in latencies when broken down by stimulus side.

Pierrot-Deseilligny et al (1991) reported bilateral increases in prosaccadic latencies in a group of patients with lesions to the posterior parietal cortex. However, in a group of patients with a right hemisphere lesion, including patients with parietal involvement, I have demonstrated no group differences in latencies. The present findings are however in keeping with the report of Ro et al (2001) who reported no difference in saccadic latencies for parietal patients making ipsi- or contralesional prosaccades in the simultaneous presentation condition of their saccadic temporal order judgement task. The results are also in keeping with the findings of Machado and Rafal (2004a).

Machado and Rafal (2004a) studied healthy older adults, a group of patients with damage to the frontal lobe including the frontal eye fields and a group of patients with damage to posterior association cortex where all but one had damage that involved the intraparietal sulcus. The task set by Machado and Rafal was to make a prosaccade to a stimulus from a central fixation cue that was in some cases predictive of target direction. Results for the FEF group indicated that this group demonstrated a field asymmetry in saccadic latencies, namely that saccades towards ipsilesional targets had longer latencies than those towards contralesional targets. The posterior group however demonstrated no field asymmetries with regard to latencies. Machado and Rafal (2004a) report, possibly due to a role of the parietal lobe in transferring attention, that the benefit of the informative cue appeared to be smaller in the posterior group compared to the healthy or frontal group.

In a prosaccade task, Ro et al (2001), however, did report, for both parietal and frontal patients, that contralesional prosaccades were more hypometric. In the present study, the amplitude of prosaccades for the three groups was also examined, and in this analysis no significant effects were

observed, although there was a trend for a difference between the groups in terms of overall saccadic amplitude size. For both patient groups, individual observations indicate that the majority of patients tend to make larger ipsilesional prosaccades, although contralesional prosaccades were generally not hypometric, with the mean accuracy of the cortical group only on average a tenth of a degree lower than the control group. Therefore whilst it could be argued that for the present study contralesional prosaccades were more hypometric relative to ipsilesional prosaccades, the amplitudes of the patients were accurate. Indeed a post hoc Wilcoxon signed ranks test focussing purely on the patients left and right saccadic amplitudes indicated no significant difference.

Rafal (2006) comments on an unpublished work from his group, were patients with chronic lesions to parietal cortex, involving in some cases the superior parietal lobule or intraparietal sulcus and in others the tempero-parietal junction, were tested in their ability to generate stimulus driven or voluntary saccades. Latencies for stimulus driven saccades were longer for contralesional targets, consistent with the findings of Pierrot-Deseilligny et al (1991). However, the deficit was also observed when button presses were required rather than saccades, and was present only in a group whose lesions involved the temperoparietal junction. Rafal argues that lesions of parietal oculomotor cortex are not necessarily involved in deficits related to stimulus driven saccadic programming. Specifically, Rafal argues that the role of parietal oculomotor cortex "is not primarily involved in commanding the initiation of either voluntary or reflexive eye movements. Rather, its function is to mediate visuomotor transformation that processes visual information into a representation that can be used to guide voluntary actions".

Antisaccade condition

In the antisaccade condition I measured patients ability to both inhibit an eye movement to a single stimulus flashed peripherally upon the screen and instead to generate a volitional saccade in the opposite direction, away from the stimulus and into the empty half of the display. Again, overall performance accuracy was quantified in terms of error rate, and compared to the 99% confidence interval of the control groups performance, all but one cortical and one subcortical patient were observed to be impaired in the task, with error rates as high as 90% observed in both groups. Surprisingly however, group analysis indicated that only the cortical group of patients was significantly different from the control group. However, a strong trend to a significant difference between the control group and the subcortical group was also observed and no significant difference was observed between the cortical and subcortical groups error rates, which in tandem with the findings from the confidence interval analysis, provides evidence for dysfunction in the task in the subcortical group also. Performance in the antisaccade test was also examined with regard to spatial modulation of error rates. Again, confidence interval analysis indicated that the majority of patients were impaired when making antisaccades into both left and right space, away from both ipsi- and contralesional stimuli. Analysis of group performance by side indicated no main effect or interaction involving stimulus side, only a significant difference in group error rates, indicating the same pattern of performance observed in the overall error rates. Importantly, neither an analysis of overall error rates or that conducted broken down by stimulus side indicated any significant difference in error rates between the two groups of patients.

Therefore, in line with the findings of the fixation condition, I have observed significantly inflated error rates in the antisaccade task in patients

such as JC, JS and HM, whose lesions spare the frontal lobe, and in patients such as GM, MK, LM, JQ and BM who have subcortical lesions. Of the cortical patients, JS and HM, and of the subcortical patients, MK, LM, and JQ have demonstrated significant impairment in both tasks. Were these patients to have shown impairment in the antisaccade task only, it would have proven more difficult to conclude whether the patients had a difficulty with suppressing an involuntary saccade or in generating an antisaccade, however, their dysfunction in both tasks adds more weight to the view that they have a dysfunction in their ability to suppress an erroneous prosaccade in the face of an irrelevant distracter, in line with their performance in the studies presented in chapter 3, were all of the patients with dual impairment in the present task with the exception of MK demonstrated inhibitory dysfunction.

A quite strict definition of a corrective antisaccade following an erroneous prosaccade in the antisaccade condition was adopted, namely that this corrective saccade had to cross the centre of the screen into the side opposite the stimulus. The vast majority of the control group's errors were corrected. With regard to patient performance correction rates varied from 39% to 100%, with all but two patients correcting more than half of their errors. Of particular interest is the finding that many patients made extremely fast corrective saccades, as fast as, and in some cases faster than latencies to initiate stimulus driven saccades in the prosaccade condition. Furthermore, all patients had shorter latencies to initiate corrective antisaccades than their latencies to generate correct antisaccades in successful trials.

Of those patients who have a reasonable number of corrective antisaccades, patient TH was observed to make corrective antisaccades in a range that is within the realms of express saccades, being 270% faster than his stimulus driven correct prosaccades and 340% faster than his correct

antisaccades. Furthermore, patient HM, for example, was observed to make corrective antisaccades 184% faster than her correct antisaccades, whilst of particular note within the subcortical group of patients was patient MK, who made corrective saccades 354% faster than her antisaccades in correct trials and 148% faster than her correct goal driven prosaccades in the prosaccade condition. Additionally, further patients can be seen to demonstrate impressive differences in speed in initiating corrective antisaccades, particularly with regard to a comparison with their correct antisaccade trial latencies.

Indeed these findings fit well with the arguments of Massen (2004) related to parallel saccadic programming. In line with the view proposed by Godjin and Theeuwes (2002), Massen postulated that evidence for the programming of parallel reflexive prosaccades and voluntarily initiated goal driven antisaccades could be experimentally manipulated. Massen argued that, in the antisaccade task, an involuntary prosaccade is programmed automatically whilst concurrently an antisaccade is being programmed. If the stimulus driven program wins out, it does so with a very small lead and thus corrective antisaccades will quickly follow. By manipulating the probability of an antisaccade trial occurring in a mixed block of pro- and antisaccades, Massen reported that antisaccadic latencies did indeed increase when the probability of their occurring decreased, which was not the case for prosaccades. Massen interpreted this finding to indicate that the slowing of the endogenous saccade, through the manipulation of expectancy, results in the stimulus driven reflexive saccade more often winning the competition between the two saccade programs. Furthermore, Massen reported on the hypometricity of many incorrect prosaccades in antisaccade trials, which she argues, are a result of the interference of the second saccadic program.

Additionally, she argued, the extremely short latencies of many corrective antisaccades following erroneous prosaccades could not be the results of a sequential programming of two saccades. Further parallels between the present study and the arguments of Massen can be seen in the reduced metrics of erroneous prosaccades compared to correct antisaccades observable in all groups.

Other support for Massen's view was provided in the same year by Koval, Ford and Everling (2004), who manipulated the probability of a peripheral stimulus appearing on a given side in an antisaccade task. Koval et al reported that increases of probability resulted in decreased latencies for correct antisaccades. Additionally, Koval et al reported that error rates actually increased with increasing saccade direction probability, and argued that the degree of preparatory activity is crucial for antisaccade performance.

Indeed further examination of patients latencies demonstrates two further findings that are common in the literature. Firstly, antisaccade latencies are higher than correct prosaccade latencies, and secondly that antisaccade latencies are higher than erroneous prosaccade latencies.

With regard to saccadic amplitudes in the antisaccade task, part of the instructions provided to patients requested them to initiate an antisaccade to approximately the same place in the empty side of the screen as the stimulus was from the centre. The control group was remarkably adept at this instruction, given that the mean distance of their antisaccades matched exactly the distance out from fixation of the stimulus. With regard to the patients, it can be seen that many patients, even when they were producing correct antisaccades, had difficulty in meeting this additional criterion of the task. Indeed compared to the confidence interval of the control group, for correct trials, many cortical and subcortical patients who were amongst the

top scorers of the patients, still produced antisaccades that were either hyper- or hypometric when producing correct antisaccades. Of note with the patients is the disparity between tendencies to make either larger ipsilesional or contralesional antisaccades. In the cortical group, TH, HM and JB make larger ipsilesional antisaccades whilst JC and JS make larger contralesional antisaccades (patient JM did not have enough trials to make this calculation in any way meaningful). In the subcortical group MK, LM, AA and BM make larger ipsilesional antisaccades whilst GM and JQ make larger contralesional antisaccades.

Additionally, the majority of the patients studied demonstrated a severe bilateral impairment on the antisaccade task with regard to error rates. Such deficits have been described before for frontal lesions. Walker, Husain, Hodgson, Harrison and Kennard (1998) describe such a patient, with a right frontal lobe infarct, who had recovered neglect at the time of testing. Although he demonstrated inhibitory dysfunction, predominantly contralesionally, on several oculomotor tests, his impairment was most profound on an antisaccade task, where he was completely and bilaterally unable to inhibit prosaccades, and least impaired in a task requiring the patient to maintain central fixation and ignore peripheral stimuli. However, the present study has reported severe deficits in an antisaccade task in patients whose lesions spare the frontal lobe.

Indeed the present results are not in line with the findings of Machado and Rafal (2004), who studied antisaccadic performance in a group of patients without neglect who had chronic lesions to the frontal lobe (including the frontal eye fields) or posterior association cortex (including the intraparietal sulcus). No group differences in accuracy were observed and all groups were able to use a predictive cue to reduce errors. Compared to the present study

however, Machado and Rafal included parietal patients whose lesion chronicity ranged from 2.5 to 29 years. Therefore, many patients in the group examined by Machado and Rafal had lesions who were far more chronic than those patients included in the present study. Patient JS in the present study for example was only six months post stroke, whilst another patient who demonstrated impairment in the present task, HM, was more in line with the post stroke status of some patients included in the Machado and Rafal study.

However, in the present study I observed little evidence of a spatial modulation to antisaccadic error rates. Whilst Machado and Rafal reported from the results of their antisaccade task that patients whose lesions involved the frontal eye field made more errors towards contralesional than ipsilesional stimuli, they also reported that patients whose lesions involved the intraparietal sulcus made more errors towards ipsilesional than contralesional stimuli. Machado and Rafal report that this is in keeping with a view that parietal lesions result in the suppression of reflexive gaze towards contralesional stimuli relative to ipsilesional stimuli.

Additionally, Machado and Rafal (2004) reported that the group whose lesions involved the intraparietal sulcus generated slower saccades away from stimuli that appeared in the contralesional field compared to those directed away from stimuli in the ipsilesional field. Unfortunately the present study did not yield enough successful antisaccade trials to permit meaningful group analysis of the laterality of SRT, but it can be seen from the means of the cortical group of patients that there is little evidence of this trend in the successful antisaccade latencies. However, it should also be borne in mind that the lesion profile of the patients in the present study was not designed to match the group recruited by Machado and Rafal.

On the basis of their findings, Machado and Rafal (2004) speculate that intraparietal cortex is responsible for the transformation of sensory information into preparation for action. Machado and Rafal argue that their findings are in keeping with the observations of Gottlieb and Goldberg (1999) that neurones in monkey LIP encode the location of contralateral signals rather than directing motor activity. In an antisaccade task with monkeys, Gottlieb and Goldberg studied neural activity in monkey LIP and reported that most neurones reacted to the location of the cue stimulus. Gottlieb and Goldberg described the role of LIP as being that of a describer of the salient world, whilst areas such as the frontal eye field decide how and when to act in this world.

Related to this Ro, Rorden, Driver and Rafal (2001) argued that the human inferior parietal lobule (and likely involving the lateral intraparietal region) is involved with saccade generation in a way that is independent of conscious perception, given the dissociation between hemifield biases in the two tasks they examined, with the critical region possibly involving the lateral intraparietal region. Ro et al studied the performance of patients with lesions to the inferior parietal lobule or dorsolateral prefrontal cortex (including the frontal eye field). When an ipsi- and contralesional stimulus appeared simultaneously, only the parietal patients demonstrated with a saccade that the ipsilesional stimulus caught their attention first more often, whilst when the decision was made with a button press, no biases in either group were observed. Machado and Rafal (2004) point to Ro et al's (2001) findings as being consistent with the notion that the parietal lobe is involved in programming voluntary saccades by using contralesional visual signals rather than purely perceptual processing (as they did not indicate asymmetry with button presses that one stimuli came first more often).

Zhang and Barash (2000) reported evidence implicating neurones in monkey LIP in computing a sensorimotor transformation (a vector inversion) prior to the performance of an antisaccade. 'Visual' neurones were identified that were characterised by a brief and early discharge close to stimulus onset, whilst 'motor' neurones were identified through a discharge later after stimulus onset toward the time of saccadic movement. However, 'paradoxical activity' was identified in some cells which could be indicative of a remapped visual response to the oppositely directed stimulus. Such cellular behaviour is in keeping with the findings of Everling et al (1998) who reported a shift of negative potential across parietal hemispheres. Zhang and Barash (2004) provide further support for the notion that neurons in monkey LIP are involved in the computation of antisaccade sensorimotor transformation in memory antisaccade tasks.

Following from these findings, Medendorp, Goltz and Vilis (2005) conducted fMRI imaging in healthy human subjects with specific focus on the posterior parietal cortex, taken as a speculated homologue of monkey LIP, whilst subjects performed prosaccades and antisaccades. Event related imaging results indicated that posterior parietal cortex actually encodes and stores the location of the eye movement goal, rather than the position of the stimulus. However, Medendorp et al do not discount the relevance of frontal areas, noting that the decision to make an antisaccade may also be a function of the frontal lobe. Indeed the results of Connolly, Goodale, Goltz and Munoz (2005) provided evidence that saccadic latencies were related to frontal eye field pre-target activity, with no observation of preparatory activity in the intraparietal sulcus.

Gaymard, Lynch, Ploner, Condy and Rivaud-Péchoux (2003) studied the performance of humans with lesions to the anterior or posterior internal

capsule compared to a healthy older adult group. Results indicated that the posterior group made less accurate saccades contralaterally in a task were prosaccades were elicited unpredictably to one side or the other, but this was not the case when the side of the target was known in advance. Additionally, all patients had normal saccadic latencies, which Gaymard et al took as evidence that the parieto-tectal pathway carries a sensory and not a motor signal.

Additionally, a proportion of patients were reported to demonstrate significant bilateral errors in an antisaccade task. Gaymard et al proposed that an interruption of parieto-tectal fibres had an adverse effect on reflexive shifts of visual attention, whilst internal shifts of attention (in the predictable task) towards a remembered location are carried through different pathways. Thus, they proposed that fronto-tectal pathways are involved in non-visually guided saccade triggering. Gaymard et al proposed that the internal capsule does contain fibres that are relevant for reflexive saccadic inhibition, fibres that are set apart from the parieto-tectal fibres. They propose that this is a third pathway, not related to either reflexive or volitional saccade accuracy related to a connection between the dorsolateral prefrontal cortex and its inhibitory control of the colliculus. The model proposed by Gaymard et al for control of visual shifts of attention features LIP-collicular neurons allowing reflexive shifts of attention and prefronto-collicular neurons involved in the cancellation of such reflexive saccades.

However, although Zang and Barash (2000, 2004), Gottlieb and Goldberg (1999) and Machado and Rafal (2004) together provide evidence for the involvement of the parietal cortex in the detection of, and subsequent remapping of a visual signal required for an antisaccade, whilst the report of Everling, Spantekow, Krappmann and Flohr (1998) provided further evidence

of a hemispheric change in activity across posterior sites, two problems with the present findings remain.

Firstly, although not matching the lesion profile of the patients reported by Machado and Rafal (2004), I found no evidence of the asymmetries they reported and conversely found elevated error rates in the antisaccade task, which they did not report. Secondly, the present results also provide evidence for inhibitory dysfunction in the fixation task, which did not require the generation of an antisaccade, and its corresponding requirements for posterior cortical vector inversion.

Therefore, the more parsimonious interpretation of the present data is that the patients are unable to inhibit a prosaccade rather than generate an antisaccade. This interpretation is also supported by the findings that the majority of the patients, the majority of the time, make extremely fast corrective antisaccades following an error.

Indeed, Pierrot-Deseilligny et al (2003) proposed that uninhibited parietal eye fields are responsible for the generation of error saccades in the antisaccade task, and the profile demonstrated by many patients in the present study is that of disinhibition in both the antisaccade and fixation task. Pierrot-Deseilligny et al argued that the inhibitory aspect of the task arises in the dorsolateral prefrontal cortex, whilst the correct antisaccade is directed by the frontal eye field. It could therefore be the case that individuals with posterior lesions have a deficit in inter lobe communication from frontal areas to parietal areas involved in the correct performance of the antisaccade task.

Chapter 5

The aim of this thesis was to explore questions relating to the use of eye movements in perceptual biases and inhibition in healthy participants and patients with right hemisphere lesions. A series of experiments were conducted which I shall summarise in this chapter and then go on to address methodological and theoretical questions relating to these studies.

A relationship between biases and eye movements

In experiment 1 the question was asked: 'Are the perceptual biases found in chimeric face processing reflected in eye movement patterns', the answer to which was an unequivocal yes. The study proposed that the diverging results produced by previous work examining eye movements to chimeric faces may be due to the varying realism of the stimuli employed. To that end I employed realistic single gender and subtly blended gender chimeric coloured faces to examine perceptual biases and simultaneously examine eye movement patterns whilst participants made gender decisions to the stimuli.

In line with previous findings, a significant leftward perceptual bias was observed, which demonstrated that the participants were behaving in line with results obtained in previous studies including Burt & Perrett, 1997; Luh, Rueckert & Levy, and 1991; David, 1993. With regard to the eye movement patterns, it was observed that the majority of first saccades were made to the left side of the stimuli shown. If leftward perceptual biases are argued to be the result of a right hemisphere bias for the processing of facial information then this finding is somewhat paradoxical as it means that initially the face is more strongly projecting to the right hemisphere. I proposed an interpretation

whereby this effect is due to the initially higher salience of the side of the face which projects to the right hemisphere at the start of the trial.

Overall my analysis reported no significant asymmetry related to the proportion of fixations in each trial to the left or right side of stimuli. However, when examining the *fixation proportions* in more detail, I reported that a relationship emerged between the gender decisions made to stimuli and the fixation proportions. In other words I reported a relationship between the perceptual biases observed and participants eye movement behaviour. I reported a significantly greater proportion of leftward saccades in trials with a left perceptual bias compared to a right perceptual bias. Similarly, with regard to the *time spent fixating* on a given side of the image, on average it was observed that participants spent an equal amount of time fixating on each side of the image. However, when the results were examined with regard to trials were the left or right side of the chimeric image was used to make the final gender decision, I reported that participants spent significantly more time fixating on the left half of the screen in trials were they based their gender decision on the left side of the face.

I proposed that, as no overall leftward eye movement biases were observed, the results therefore argue against a left to right reading direction based scanning bias. However, an overall interpretation of the findings was discussed were right hemisphere cortical mechanisms may be possibly said to interact with a bias related to reading direction.

Orientation

Experiment 2 investigated whether a left perceptual bias could be obtained with facial stimuli that were inverted. Research was reviewed which relates to the stance that such stimuli are not thought to be processed in the

same way that upright faces are processed, due to differences in factors including expertise and configuration. Additionally some equivocation in this issue was suggested. To investigate this issue the same single gender and chimeric faces were employed in a further gender identification study, with all images shown both upright and inverted.

Results of experiment 2 indicated that participants were more accurate at identifying the genders of single sex faces when they were upright. Additionally, we obtained a significant leftward perceptual bias for gender decisions to chimeric stimuli in the upright condition, whilst the same analysis for inverted stimuli was not significantly higher than chance. Furthermore, the perceptual biases in both conditions significantly differed form each other. However, two participants responses were observed to be atypical in their responses, and when these scores were extracted from the data set it was observed that the leftward biases observed for inverted faces proved to be statistically significantly different from chance.

Experiment 2 therefore replicated experiment 1 in demonstrating the finding that participants significantly more often use the left side of the image when making gender decisions after exposure to chimeric stimuli. Additionally, experiment 2 provided evidence that this effect could be shown to survive when the faces were inverted. However this was only the case when two participants who proved to be experimental outliers were removed from the dataset. Moreover, the analysis indicated that the leftward perceptual bias obtained was reduced relative to that displayed for upright faces. It was proposed that the participants may have adopted a simplified configurational judgment or focussed their attention preferentially on a single feature of the left side of the inverted image. However, such an interpretation would only

stand if it were the case that participants in this study preferentially viewed such features on the left side of the face.

Biases without eye movements

Beginning with the proposal of Ferber and Murray (2005) that eye movement patterns are dissociated from perceptual biases to chimeric faces, I then turned to examine this issue by attempting to obtain a significant left perceptual bias with the stimuli employed in experiments 1 and 2, but presented at a brief exposure duration of 100 milliseconds. It was proposed that this very brief exposure duration would prevent any significant volitional saccades to be made to the stimuli. In experiment 3 I was again able to demonstrate that the participants who took part in the task significantly more often based their gender decisions to the chimeric faces on the information available on the left side of the face. However, an independent samples t-test was conducted to compare the magnitude of the leftward bias to chimeric facial stimuli obtained in experiments 1 and 3. The result of this test indicated that the magnitude of the leftward bias was significantly reduced relative to the bias obtained in experiment 1 which employed a larger (2000 millisecond) exposure duration.

Therefore the result of experiment 3 indicates that it is possible, in line with Ferber and Murray's argument, to dissociate perceptual biases to chimeric faces from eye movements. However, the t-test analysis referred to above indicates a reduced bias with a brief exposure duration which precludes eye movements relative to the longer exposure duration in experiment 1. This was proposed to indicate that the bias is significantly stronger when eye movements are possible. The results further suggest (when considering together the findings of both experiment 1 and experiment 3) that when a

preferred scanning direction can be employed, such a deployment would preferentially increase the salience of left hemi-field stimuli, leading to increased perceptual biases to this side of space. This proposal was therefore investigated in experiment 4. In experiment 4 I turned next to examine the question of whether or not a systematic increase in presentation time, which would allow a related increase in eye movements, would lead to an increase in the perceptual biases obtained from chimeric facial stimuli.

Additionally in experiment 4, a group of healthy older adults were recruited, in order to examine the effects of healthy aging on perceptual biases to chimeric faces. Evidence was reviewed which suggests that tasks which selectively engage the right hemisphere may be executed in a different fashion in an elderly compared to a younger sample of participants, either related to selective right hemisphere aging or an age related reduction in hemispheric asymmetry. Additionally however, literature pertaining to chimeric face studies with older adult samples was reviewed, which indicated that evidence to date has not been strong to indicate age related differential performance in paradigms involving chimeric faces. However, a recent study by Failla et al (2003) demonstrated an age related change in perceptual bias. Moreover, it was pointed out that the studies reviewed which had investigated this issue had used spliced photographs as stimuli, and experiment 4 was designed to investigate this issue with the more lifelike stimuli employed in experiments 1-3.

Experiment 4 employed three separate exposure durations, a free view condition, a 300 millisecond and the 100 millisecond condition employed in experiment 3. It was anticipated that the degree of leftward perceptual bias obtained in the experiment would be higher in a free view condition compared to the 100 millisecond condition, if the freedom to preferentially saccade to the

left of the image was allowed with a longer exposure duration. It was also anticipated that the realistic stimuli employed would allow for a truer account of the perceptual processes at work in chimeric face processing with older adults. A group of younger and a group of older adults were thus tested with the three experimental conditions.

A significant factor in this study was the participant's accuracy, which was deemed to be particularly important in order to rule out age differences due to the quality of participant's eyesight. Particularly in the event of older adults demonstrating chance performance in the shorter exposure durations, it was deemed important to be certain this result was related to diminished perceptual bias and not regression to the mean as a result of guessing. This resulted in seven older adults (and two younger adults) being omitted from subsequent analysis due to single gender determination being at chance level.

Results of experiment 4 indicated that older adults were less accurate at single gender identification overall, but that both groups were equally accurate in the free view condition only. With regard to perceptual biases, the older adults responses in the 100 millisecond condition were found not to differ from chance, but all other comparisons showed a degree of leftward perceptual bias which were significantly higher than chance level and therefore indicated a reliable leftward perceptual bias. The results of group and condition comparison, by means of ANOVA were interpreted to indicate that the older adults had a reduced bias overall, and at the shortest exposure duration the bias of this group did not differ from chance levels, with the degree of leftward bias demonstrated by both groups increasing with exposure duration. Additionally, the results were interpreted to suggest that the bias of the older adults continued to increase with exposure duration, whilst the bias of the younger group was approaching ceiling level at 300 milliseconds of

exposure. Therefore the prime hypothesis that an increase in exposure time would lead to an increase in perceptual bias was supported by the results of experiment 4: whilst a significant leftward bias was obtained in the younger adults group with a very brief exposure duration, in replication of experiment 3, it was also observed that the free view condition led to a significantly higher degree of perceptual bias.

With regard to reaction times in experiment 4, interestingly, no differences were observed between the two age groups in terms of latencies to make gender decisions. It was suggested that, when considering the accuracy results and the latency results together for the older adult group, that this would point to an interpretation whereby the older adults sacrificed accuracy for speed. Therefore the main findings of experiment 4 were evidence of a temporal component to perceptual biases to chimeric stimuli, and that younger adults demonstrate higher levels of perceptual bias than older adults. Indeed only in younger adults can such biases be observed at sub-saccadic stimuli exposure thresholds. Thus the proposal of Ferber and Murray (2005) appears to be more applicable to younger adults, whilst older adults appear to demonstrate reduced right hemisphere function in the task.

Inhibition, capture and search

Experiments 1-4 examined issues related to biases to scan leftward when healthy participants were exposed to chimeric faces, and additionally proposed a right hemispheric dominance in the task as a driving force behind the results obtained. Experiment 5 reviewed evidence that demonstrated dysfunction in visual search in patients with lesions to the right hemisphere related to difficulty in searching the full extent of a visual array and in generating saccades to particular areas of a visual search array. Whilst this

has been studied previously, what is much less understood is the question of how well such patients are able to inhibit a response to an irrelevant stimulus in what would otherwise be a very simple visual search task.

Experiment 5 examined simultaneous top down and bottom up influences on occulomotor capture by employing an adaptation of the paradigm employed by Ludwig and Gilchrist (2002). Although evidence to date indicates that patients with right hemispheric lesions are impaired in visual search tasks, experiment 5 was designed to examine whether impairments would be demonstrated in a task were participants would be required to inhibit eye movements to irrelevant distracters. The experimental paradigm involved the participant searching for a red target amongst green distracters, which would appear in predictable locations. Additionally, in onset trials an additional distracter would appear in an unpredictable location, whilst in no-onset trials this additional distracter would appear in a location previously occupied by a placeholder. Additionally, this additional distracter would be either similar or dissimilar in colour to the target. Thus the paradigm involved trials where the additional distracter had a similar onset, similar no-onset, dissimilar-onset or dissimilar no-onset. The paradigm was first applied to a comparison of the performance of a group of healthy older adults and patient TH, a 73 year old man with a right tempero-parietal lesion, with sparing of the frontal lobe and no evidence of visual field dysfunctions.

Results indicated that the patient demonstrated increased overall occulomotor capture by the irrelevant additional distracter relative to the control groups performance. Comparing levels of capture (the proportion of first saccades made to the additional distracter rather than the target) indicated that the patients rates of capture were seriously effected by the similarity of the additional distracter to the target in three out of four possible

target-distracter spatial combinations. Thus, although such an inability to inhibit a response is frequently demonstrated in patients with frontal lobe lesions, experiment 5 demonstrated a similar deficit in a patient with a lesion sparing the frontal lobe. This finding was proposed to suggest that with regard to eye movements, successful inhibition of a response also requires the intact functioning of posterior cortical areas.

Even more serious disruptions in target search were observed when the impact of the sudden onset of the distracter was examined, as in all four possible target-distracter combinations the patient demonstrated elevated levels of occulomotor capture. In terms of overall levels of capture, and capture in terms of the similarity of the distracter to the target, it was observed that the performance of the patient was in line with that demonstrated by the control group in the condition where the target was on the right hand side and the distracter was on the left hand side, which was the location that would be expected to result in an extinction like effect. Such an effect is observed in individuals with, or recovering from, hemispatial neglect, whereby a single left stimulus may be seen, but may no longer be observed if a competing right stimulus is simultaneously presented. The lack of this extinction like effect in terms of onset based capture was taken to suggest that such processing happens before the influence of the patients spatial deficit occurs.

The finding of increased levels of overall capture in patient TH was proposed to suggest that with regard to eye movements, successful inhibition of a response requires an intact functioning of posterior cortical areas. To further explore this proposal, experiment 6 went on to test a larger group of patients with the same paradigm, and compare their performance to the healthy control group's results. Therefore a group of patients with cortical

right hemisphere lesions and subcortical right hemisphere lesions was tested with the same experimental design.

Examining the performance of the control group in experiment 6, it was observed that they performed very much in line with the younger group of participants reported by Ludwig and Gilchrist (2002), in that the effect of capture was particularly pronounced when the additional distracter was similar to the target, and particularly when the additional distracter appeared with a sudden onset.

Group analysis comparing the performance of the control group, cortical group and subcortical group indicated that the overall rates of occulomotor capture were significantly higher for both patient groups relative to the control group, whilst the patient groups error rates did not significantly differ. Additionally, it was observed that the effect of the onset of the additional distracter interacted with group, which broke down to reveal that when the additional distracter appeared with a sudden onset, the error rates of the cortical group were significantly higher than those of the control group (this analysis also revealed a trend to the same difference between the control and the subcortical group).

When a 99% confidence interval of the overall error rate of the control group was generated to examine the individual error rates of the patients, it was observed that the majority of the cortical group of patients and half of the subcortical group were reliably impaired relative to the control group, in terms of their overall error rates. Additionally, in line with the single case study, measures of the degree of the influence of the similarity and the onset of the additional capture were obtained for the patients and compared to 99% confidence intervals of the control group. Analysis of capture with regard to the similarity of the additional distracter revealed that only patient TH,

described in the previous section, and an additional subcortical patient (LM) were reliably impaired relative to the control group. Finally, analysis of capture rates with regard to the onset of the additional distracter indicated that relative to the 99% confidence interval of the control group, half of the cortical group and one third of the subcortical group were reliably impaired.

Regarding spatial modulation of capture rates, reliable group differences in the spatial modulation were observed in that significant differences in error rates were observed between left and right targets for both the cortical and subcortical groups of patients, with higher error rates for both groups with left targets.

Whilst the evidence reviewed in this chapter makes it clear that frontal structures are vital for the suppression of unwanted saccades, the results of experiment 6 clearly indicate significantly higher distractibility in a group of patients with right hemisphere lesions (including patients whose lesions spare frontal structures). Additionally the results provide some evidence for a spatial modulation of this distractibility effect. To examine this claim further, the same patients were invited back to the laboratory to test their occulomotor inhibitory capabilities in a further set of studies.

Experiment 7 examined separately the ability of the two patient groups to generate stimulus driven prosaccades, inhibit all occulomotor responses and thirdly to inhibit a stimulus driven prosaccade and instead generate a voluntary antisaccade. To this end, three separate prosaccade, fixation and antisaccade blocks were run. The performance of the patients in the antisaccade task was thought to be particularly of interest as this task is frequently reported to generate high error rates in patients with frontal lobe pathologies. However, evidence was also reviewed pointing to posterior, and parietal, involvement in this task.

Analysis of the prosaccade condition demonstrated that all three groups had no difficulty in generating stimulus driven saccades to a peripheral target. Additionally, all three groups performed the task with comparable latencies to initiate the prosaccade, a finding which was in contrast to that reported by Pierrot-Deseilligny et al (1991) in a group of posterior parietal cortex lesioned patients. In line with Ro et al (2001) however, the analysis also indicated no differences in saccadic latencies within the patient groups to initiate leftward or rightward prosaccades. Additionally, no significant differences in the overall accuracy of the amplitude of the saccades made by any group were observed. When amplitude accuracies were examined with regard to saccades to left and right targets however, it was observed that leftward saccades, relative to the control group, were significantly shorter in the subcortical group.

Results from the fixation condition, where the participants had to maintain central fixation and ignore peripheral distracters complemented the findings from experiment 6, in that relative to the control group, the cortical group were significantly more distracted by the peripheral stimulus when attempting to maintain central fixation throughout the task. This analysis also indicated a trend for the subcortical group to also demonstrate significantly higher distractibility. Individual patient comparisons were made to the 99% confidence intervals generated from the results of the control group, which demonstrated that all but one cortical patient were significantly more distracted by the peripheral stimulus than the control group. Additionally, confidence interval analysis indicated that half of the subcortical group was also reliably more distracted than the control group. The performance of some patients in the fixation condition clearly indicated that patients whose lesions spare the frontal lobe have difficulty in suppressing an

eye movement, indicating that they have an inhibitory dysfunction, or that the inhibitory capacity of their frontal lobe is not being correctly signalled.

Finally, analysis of the antisaccade condition complemented the findings of the fixation condition in demonstrating significant impairments in the patient groups. A confidence interval of the error rate (which was defined as an erroneous prosaccade towards the peripheral stimulus) of the control group in the antisaccade task was calculated, and compared to this, all but one cortical and one subcortical patient displayed inflated error rates in the task. Whilst the subcortical patient who was unimpaired overall was somewhat younger than the rest of the patients and demonstrated no clinically obvious sign of his subcortical lesion, the cortical patient who was unimpaired was, surprisingly, patient TH who demonstrated impairments in the single case study of experiment 5. Additionally, group analysis indicated that as a whole, the cortical group of patients demonstrated significantly higher overall error rates in the task compared to the control group, whilst a strong trend to a significant difference was also observed with regard to the elevated error rates of the subcortical group relative to the control group. Whilst such elevated error rates have been observed in frontal patients, they are not in line with the findings of Machado and Rafal who found no evidence of lower accuracy in a group of patients with lesions to posterior association cortex (although it was observed that the patients Machado and Rafal reported on were more chronic as a whole).

In the antisaccade condition, analysis of the data also focussed on possible differences in performance between left and right stimuli (which would require, respectively, right and left antisaccades to successfully complete the trial). Surprisingly, when compared to confidence intervals of the control group, all but one cortical patient who had been observed to be

impaired overall with regard to error rates were also found to be impaired for trials involving both left and right stimuli. Additionally, this pattern was also observed in some subcortical patients, although the pattern was less systematic in this group. Furthermore, group analysis, broken down by stimulus side, indicated again significantly higher error rates in the cortical group of patients (and again a strong trend to a similar pattern with regard to the subcortical group), but no evidence of any interaction of error rates and side of the stimulus. These findings were again not in line with the report of Machado and Rafal (2004) who interpreted their findings of increased errors towards ipsilesional stimuli as evidence that parietal lesions result in the suppression of gaze towards contralesional stimuli.

However, a comparison of the amplitudes of antisaccades between the three groups, again by means of confidence intervals of the control group, indicated that for both left and right stimuli that patients were less accurate in their antisaccades, making either hyper or hypometric antisaccades.

With regard to the question of whether or not participants, when making an erroneous prosaccade in the antisaccade task demonstrated a secondary corrective antisaccade, it was revealed that this was the case in the majority of errors involving the control group, and was also the case that the majority of patients corrected the majority of their errors. Interestingly, analysis of the saccadic latencies of corrective antisaccades following erroneous prosaccades indicated that they were made extremely quickly. These observations of extremely fast corrective antisaccades were observed to complement the findings of Massen (2004) who related them to parallel programming of reflexive and voluntary saccades.

The results as a whole showed that adding a fixation condition to complement the findings from the antisaccade condition was a useful

measure, as the antisaccade task requires both the ability to suppress an involuntary stimulus driven saccade and also to generate the antisaccade afterwards. It would have been problematic to deduce which of these two steps the patents who demonstrated impairment in the antisaccade task found problematic. However, the impaired performance in the fixation condition strongly suggests that the impaired patients have difficulty in inhibiting a saccadic response to a suddenly appearing peripheral stimulus. Indeed taken as a whole it was observed that two cortical (whose lesions spared the frontal lobe), and three subcortical patients had significant impairment in both the fixation and antisaccade task and demonstrate a serious impairment in their ability to inhibit a saccade to a suddenly appearing peripheral stimulus.

Therefore, whilst the evidence of Everling, Spantekow, Krappmann and Flohr (1998), Machado and Rafal (2004), Zang and Barash (2000, 2004) and Gottlieb and Goldberg (1999) point to the involvement of the parietal cortex in the remapping of a visual response, the results of experiment 7 appear to demonstrate that the patients studied have an inhibitory deficit rather than a deficit involving either detecting a salient (and subsequently to be ignored) stimulus or in computing a vector inversion to produce an antisaccade. The patients studied demonstrated no impairments in the prosaccade task when asked to make saccades to a single salient stimulus, but demonstrated significantly higher error rates in the antisaccade task. Furthermore, there appeared to be no fundamental problem with remapping the saccadic response to the other side of the screen (on the basis of their ability to make corrective saccades in the majority of trials for the majority of patients).

In both the fixation and antisaccade task the principal deficit seems to be one of inhibition. Therefore it was argued that the patients studied, whose lesions spared the frontal lobe, demonstrated impairments in exogenous

prosaccade inhibition rather than in antisaccade generation, a finding which also complements the observation that the patient groups were significantly more distracted than the control group in the capture paradigm of experiment 6.

Methodological issues

A number of methodological issues were identified during the course of the research presented in this thesis, which would have led to clearer interpretations in some cases and would possibly assist those attempting replications or derivations of the research presented here.

In experiment 1, the first chimeric faces study, the exposure duration of stimuli was set at 2000 milliseconds, an exposure duration selected on the basis that it would allow participants sufficient time to make a gender decision to stimuli that were designed to be somewhat androgynous, and thus would permit several fixations before a gender decision was made. However, a clear methodological flaw in such a design is that in many cases it is likely that eye movement data was included after the subject had made their gender decision and were waiting for the trial to time out. Additionally, we were unable to obtain any meaningful analysis of the participants last saccade as they made their gender decision, in order to examine whether this had some influence on their decision.

A further problem in experiment 1 was the clear gender bias in the participants, a classic demonstration of the gender skew in undergraduate Psychology, from whom the participants were on the whole drawn. Only four male subjects were recruited, which prevented a comparison of male and female biases. However, the main findings do not change when the four male participants are removed from the data set.

When the results of experiment 1 are examined in this way, perceptual and first saccade biases stay virtually the same, as do the other biases, although the results for number and fixation duration become non-significant (this if of course possibly due to the reduced power). With regard to perceptual bias for chimeric faces, removing the four males from the set results in 64.1% of responses being based on the left hand side of the chimeric faces (binomial test, $p<0.001$). This is actually a slightly higher bias than the original data set. With regard to the first saccade, when four males are removed from the results, when the remaining subjects showed a left behavioural bias (i.e. the left side of the face influenced the gender decision), when averaged across subjects, 75.6% of the first saccades were to the left but with a right behavioural bias 70.1% of the first saccades were still to the left.

With regard to the average proportion of total fixations, for 16 subjects the grand proportion of leftward fixations was 0.55. A one-sample t-test (against 0.5) failed to reach significance ($t(15)= 1.530, p=0.147$). Examining proportions separately for left and right perceptual biases, a paired samples t-test ($t(15)= 2.659$, $p<0.05$) indicated a significantly greater proportion of leftward saccades with a left perceptual compared to a right perceptual bias. However, in this case examining the proportion for left and right biases separately with one sample t-tests against 0.5 indicated that neither data set was significantly different from an even 50/50 distribution ($t=1.919$, $p=0.74$, $t=.746$, $p=0.467$ for left and right proportions respectively).

Similarly, with regard to fixation duration, with males removed, subjects gave no indication of spending more time on either the left or right side of the face (one sample t-test: $t(15)= 1.076$, $p=0.299$). Turning to left versus right perceptual biases, a paired sample t-test was conducted between fixation durations for left and right perceptual biases, this narrowly failed to

reach significance at the 5% level ($t(15)=2.118$, $p=0.051$). Therefore, although the observed slight differences may have been related to reduced statistical power, it would have been ideal if equal numbers of male and female participants could have been recruited to allow a full gender comparison.

Although experiment 3 was successful in providing evidence for significant leftward biases with a 100 millisecond exposure duration, it would have been beneficial to have obtained an objective measure that participants had been centrally fixating prior to stimulus onset, either through eye tracking or the use of a briefly presented central digit that the participants need to identify along with their gender decision. Furthermore, whilst considerable care to taken to match the program running the experiment to the refresh cycle of the monitor, and subsequent photoelectric diode measures were taken to ensure the stimuli were displayed for precisely 100 milliseconds, with hindsight further control over the exposure duration of stimuli could have been obtained if a backward mask of noise was displayed following stimulus offset to remove the possibility of visual persistence in experiment 3 and 4.

It also has to be conceded that the exclusion criterion of experiment 4, namely that subjects who were at chance level or below (50%) in their identification of single gender images in any of the three exposure conditions could be viewed as arbitrary. Clearly this criterion resulted in the exclusion of a significant proportion of the older adults from the data set. However, if all participants are replaced in the data set (with exception of one who did not follow instructions and one who was left handed in older adults) the results still demonstrate a main effect of condition ($F(2,86)=4.42$, $p<.05$) and age group ($F(1,43)=6.89$, $p<.05$), with no interaction ($F(2,86)=.58$, $p=.56$), suggesting that the reported age effect was still valid.

However, follow up comparisons now revealed that the left bias obtained from the 100 millisecond condition was significantly lower than both the 300 millisecond and free view conditions (both $p<.05$), and furthermore that the 100 and 300 millisecond conditions also significantly differed from each other ($p<.05$). However the mean left bias for the 300 millisecond and free view conditions did not significantly differ form each other (overall means for 100, 300 and free view conditions 53.3%, 55.7% and 56.1% respectively).

Additionally, with regard to perceptual biases, one sample t-tests of older and younger adults in each of the exposure conditions indicated that with the exception of the older adults in the 100 millisecond condition ($p=.49$), all other conditions were observed to be significantly different form chance (50%) performance (older adults 300 millisecond condition $p<.05$, older adult free view condition $p<.01$, younger adults 100 millisecond condition $p<.01$, younger adults 300 millisecond condition $p<.001$, and younger adults free view condition $p<.01$), which were the same findings reported in the experiment.

Indeed, with regard to the accuracy criterion, it is quite possible that the exclusion of subjects who were at or below 50% accuracy may have unnecessarily weakened the power of the study. Additionally, it has to be conceded that the figure of 50% is somewhat arbitrary. To address this methodological issue, t-tests against chance performance were conducted on the mean accuracy for single gender male and female faces separately for both groups, for all three conditions, with all subjects (with the exception of two older adults omitted for other reasons than accuracy as outlined above). All twelve conditions examined proved to be significantly different from chance performance (all $p<.001$), indicating that each group's accuracy was significantly above chance.

A final methodological consideration is common to all four studies employing chimeric faces, and pertains to the use of androgynous like facial stimuli in the studies. It is distinctly possible that perceptual biases have been underestimated in the reported effects. Whilst androgynous like facial stimuli increase the yield of eye movements initiated by participants, which was an important consideration for the longer exposure conditions in experiments 1, 2 and 4, they also introduce a degree of error into participant's gender decisions. This error could influence the magnitude of perceptual bias obtained in the studies. In a given trial, a left perceptual bias to a female-male chimeric face should result in a participant making a female gender selection. However, if the gender of the left hemi-face is improperly identified, a male decision will be made, and therefore a right bias will be recorded for the trial. If this type of error occurs it could lead to a systematic underestimation of the overall perceptual bias. Hypothetically, if the degree of perceptual bias in a study was 100% leftward, but 20% of chimeric faces in the study were misidentified this would lead to an underestimation of the perceptual bias in a study by the same amount (i.e. a reported leftward bias of 80%). Such potential underestimations should be carefully considered in future studies, particularly when reported biases are low.

It also has to be conceded that the occulomotor capture paradigm of experiment 6 may have been overambitious in the number of factors involved, which included onset, similarity, target side and distracter side. Clearly the number of trials that can ethically be collected from patients is limited, and it may have been more prudent to reduce the number of factors in a given block to increase statistical power.

Furthermore, in experiment 7 I proposed that the deficit displayed by patients is one of saccadic inhibition and not one of antisaccade generation.

This conclusion was based on the observation that patients demonstrated impairments in the fixation task in addition to the antisaccade task. However, a firmer conclusion could have been made if an additional block requiring only saccades into an empty space in the absence of peripheral stimuli was run. This could have been achieved through a central directional arrow following fixation. Although it is anticipated that patients would not demonstrate any significant impairment in this type of task it would have been prudent to add it to the study.

Future directions

In experiment 1 I alluded to the possibility that leftward biases were due to a predominant activation of the right hemisphere by face stimuli, or by all complex visual configurations, or to the left-to-right scanning habit in reading favouring initial inspection on the left side of the image. The scanning bias effect due to reading direction is currently being examined in the laboratory of Ari Zivotofski, in collaboration with Sylvie Chokron, were it is intended to carry out the same study with a group of right to left Hebrew reading participants. An interpretation of the results in terms of a directional reading bias would predict that results would be reversed in a right to left reading population, whilst an interpretation of the results in terms of right hemispheric biases would predict similar findings to those observed in experiment 1.

However, results from this follow up study, should they support a right hemisphere bias interpretation of the results of experiment 1, would still leave open the interpretation of rightward biases being due to complex stimuli configurations in general rather than faces per se driving the right hemisphere

bias, and an eye tracking study involving participants exposed to non-facial complex visual stimuli remains to be considered.

In experiment 2 it was suggested that simplified configurational judgements, possibly on the basis of attention being focussed on a single facial feature of the inverted image could explain the existence of a leftward bias to inverted facial images. However, such an interpretation requires the assumption that the participants preferentially viewed such features on the left side of the face, and to clarify and support this suggestion a replication with simultaneous eye tracking would need to be conducted in a future study.

Finally, experiment 4 proposed that obtaining leftward biases to chimeric faces employing a gender decision may invoke mechanisms that lie closer to true face processing than those obtained with stimuli composed on the basis of emotion. However, it would be interesting to carry out a further varying exposure duration study employing such emotion based chimeric faces, in order to explore both the effect of exposure duration on perceptual biases, and also to examine how such biases relate to those obtained with gender based chimeric faces.

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